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GENETIC AND ENVIRONMENTAL FACTORS OF SHEEP UNDER ARID CONDITIONS

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I. INTRODUCTION

The ability of sheep to survive under adverse environmental conditions is one of the main reasons for their wide spread distribution. Sheep are common in near-Arctic regions such as Iceland and Finland as well as in the driest deserts of the world in Africa and Asia. In certain areas of the world, sheep are the only type of domestic animals that lives, produces, and reproduces successfully. The fact that sheep are not only able to maintain themselves under such adverse conditions, but that specialized types have been developed to produce meat, milk and wool gives them special importance. For instance, lambs are the only class of livestock that will fatten on natural grasses without grain and still meet the U.S. choice grade. On the other hand, sheep consumes roughages that often cannot be harvested as well in any other way. In addition, the wool produced by sheep has always been prized as a textile fiber because of its appearance, softness, tailorability, and heat conservation. Wool offers a combination of desirable qualities not found in any other fiber, natural or man-made.

This ability to survive and produce under hardships caused sheep to be the best suited animals to live, with minimal care and management on the Indian Reservations in the Southwestern United States.

The Navajo sheep studied here have evolved under conditions that are inferior to farm and other range conditions in the United States. They have developed characteristics for adaptability to harsh environments, fertility and mothering ability which may be of value if transmitted to other breeds of sheep.

A vast area of the world lies in arid circumstances and the inhabitants lack animal protein. The sheep breeding project at the Southwestern Range and Sheep Breeding Laboratory at Fort Wingate, New Mexico, may provide ideas and experience, as well as animals, which will be useful in many parts of the world.

One of the main purposes of this study was to investigate the relative importance of the environmental factors on the production of sheep under these arid conditions. The second main purpose was to measure the genetic and phenotypic parameters that are concerned with lamb and wool production so that breeding programs can be developed to achieve maximum progress from selection.

II. REVIEW OF LITERATURE

A. Environmental Effects on Production Traits

The ability to evaluate individuals correctly is most important for selecting future parents in order to attain maximum improvement. Both induced and natural environmental factors operate to conceal genetic merit, thereby confusing the breeder and obstructing his efforts to select those animals having the greatest breeding value. In many instances variations in environment can be eliminated or controlled, but in others only adjustment or correction is capable of placing animals on a comparable basis (Hazel and Terrill, 1945a).

An extensive literature has accumulated concerning the effects of environmental factors, particularly level of feeding, presence of mineral deficiencies and climatic conditions of temperature, humidity and rainfall on wool growth and body weight. However, under range management systems, the effects which can be identified and recorded are few in number. For a particular flock, many of the components of the local environment are fixed and are alike for contemporaries, but may vary from year to year. Factors which can be recorded are thus usually restricted to type of birth and weaning, sex, age of dam, year of birth, breed, age when observation was obtained, and percent inbreeding.

Phillips and Dawson (1940) have raised the question, whether the effects of type of birth and sex may be regarded as genetic or environmental in nature. Whether a ewe will have one or more lambs is certainly determined to some extent by its genetic make up. However, when selection is practiced for fleece and body traits, it is justifiable to consider type of birth as being an environmental effect. Two animals, one a single and the other a twin, may be of equal genetic potentiality for fleece and meat production. The influence of type of birth, however, may act as a handicap for the animal born as a twin to develop as rapidly as the single, thus giving the single an advantage over the twin to survive selection.

Differences due to such factors should be eliminated for all traits studied before selection of individuals from a given population is practiced.

1. Birth weight

The importance of birth weight as a factor in sheep production has been demonstrated by many workers. Phillips and Dawson (1940), found birth weight to be one of the factors that influenced survival, growth and selection of breeding animals to be retained in the flock. A significantly higher proportion of the lambs that were heavier at birth survived than of those lighter at birth. They also found a positive relationship between weight at birth and weight at three months of age. Accordingly it is most important to know how much of the individual birth weights are due to environmental effects in order to be able to account for them, since the progress from selection is based on the genetic superiority of selected individuals. Blunn (1943) working with Navajo sheep, found that year differences were not so pronounced at birth as at later weights. Kean and Henning (1949) reported real differences between years in their effect on birth weight. Yao et al. (1953) observed a significant year effect on the birth weight of Karakul sheep. Blackwell and Henderson (1955) stated that years were important sources of variation due to the weather and the general health of the flock. Bogart et al. (1957) found similar results. Sidwell et al. (1964) reported a study involving 4331 lambs of the Hampshire, Shropshire, Southdown and Merino breeds and their 2, 3, and 4-way crosses. Least square estimates were used to get the constants of the different sources of variation attributed to environmental factors, to breed, and to breed crosses. The analysis of variance of birth weights showed that differences between years were significant. Also fitted in their models were some of the interactions which involved years and these were found to be non-significant. Another model was also used which included only 3423 lambs representing those individuals who had both birth and weaning weights. In this analysis, the interaction between sex and high or low production years had non-significant effects on birth weights. But in all models differences between years of birth were significant. The standard deviation of birth weight of the lambs weaned, was significantly smaller than that of all lambs born (1.25 vs. 1.37 lbs). This, they added, supports the general observation that the extremely small and the very heavy lambs at birth are less likely to survive than lambs of intermediate size.

Other environmental factors affecting birth weights of lambs have been investigated by many workers. These factors include difference due to sex, type of birth, age of the dam and breed of the dam or sire. Chapman (1931) found significant differences in weight at birth due to year effects. He also found that the regression of birth weight on the age of dam was .26 pounds per year. Type of birth had the most pronounced effect, singles being 2.10 pounds heavier than twins, and the two sexes were equally affected by these factors. Single females weighed .61 pounds less than single males, while the twins of both sexes were about equal in weight at birth.

Kincaid (1943), in a study to evaluate the influence of the sire breed on birth weight of lambs, used a switch-back (reversal) design. He found that only 7.8 percent of the variation was due to the breed of sire. Hampshire sired lambs were 1.05 pounds heavier at birth than those sired by Southdowns, the difference being highly significant. He also observed that there was an annual increase of .63 pounds in birth weight of lambs as the ewe increased in age from two to six years of age, and that there was no significant departure from linearity. Nelson and Venkatachalam (1949) showed in their analysis that significant portions of the variance were due to sex, type of birth, and age of dam. Birth weight of females was 5 percent less than that of males. Lambs from mature ewes were 10 percent heavier than those from two year old dams, and single lambs weighed 22 percent more at birth than twin lambs. Kean and Henning (1949) found a real difference between years on their effect on birth weight. Males were .6 pounds heavier than females, and single born lambs weighed 1.4 pounds heavier than twins. Yao *et al*. (1953) in a study of birth weight and fur characteristics of Karakul and Karakul crosses found that breed, sire and year effects were significant.

Blackwell and Henderson (1955) made an analysis of the birth weights of 2158 lambs from the Corriedale, Hampshire, Shropshire and Dorset breeds kept under farm flock conditions in New York. The Dorset data were analyzed separately because of interest in the effect of season of lambing, which was absent from the other 3 breeds. Year differences were important sources of variation due to weather and health.

Both linear and quadratic partial regressions were fitted for age of dam effects. The linear regression of birth weight on age of dam was found to be .71 pounds for each increase of one year in the ewe's age and was significant. The quadratic term amounted to only .06 per year and, though significant, was of small size. In the Dorsets the linear term was .27 pounds and was the only significant one. Breed differences were significant. In the three breeds, males were .54 heavier than females, while singles were 1.85 heavier than twins. For Dorsets the corresponding differences were .36 and 1.20 pounds, respectively. There was a difference of .40 pounds between spring and fall lambs at birth in the Dorset breed. All of these effects were statistically significant.

Cassard and Weir (1956) analyzed factors affecting weights and growth rates of Suffolk lambs. They found that sex had no significant effect on birth weight. Single born lambs were heavier than twins and grew faster, this effect persisting longer in males than in females.

Using data on three breeds of sheep and crossbreds, Ali (1952) reported that lambs from mature ewes were .67 pounds heavier at birth than those from young ewes. In the same study singles exceeded twins by 1.75 pounds and males were .05 pounds heavier than females.

MacNaughton (1956) used data collected from the flock maintained by the Experimental Farm, Lethbridge, Alberta, Canada, on both Rambouillet and Canadian Corriedale sheep. The study involved 3039 lambs born and the method of marginal totals was used to find the effects of the different environmental factors in order to account for them by adjusting the data. The adjusting factors were made separately for each breed. He found that males were .61 and .48 pounds heavier than females. Singles exceeded twins by 1.95 and 1.78 pounds and lambs born from mature ewes weighed 0.0 and .48 pounds more than those from two-year old ewes for the Rambouillet and Corriedale breeds, respectively.

Bogart et al. (1957) used the least squares method for fitting constants to measure environmental effects on birth weight. They found no significant difference due to breed of dam. Even breed of sire effects might have resulted because the variation within breeds was large enough to overshadow the differences between breeds. Type of birth was the most dominant effect, singles being 1.92 to 2.40 pounds heavier than twins. Sex had a consistent effect, males exceeding females by between .28 and .44 pounds. They also found that the interaction between type of birth and sex was inconsistent and unimportant. They concluded that correcting data for type of birth would make possible early selection and castration of males to be marketed at weaning.

In Welsh mountain sheep Dalton (1962) analyzed data including only single born lambs, as twins were scarce. There were consistent sex and age of dam effects. The regression of lambs birth weight on the dam's tupping weight was small and non-significant.

Donald (1962) worked adjustments for each of 5 years separately. He found that males were .6 pounds heavier than females, that twins weighed 3.1 pounds less than singles, and that lambs from 1 year old dams were 2.3 pounds lighter than those from 2 year-old ewes, while the latter weighed .2 pounds less than those from mature dams.

Yalcin and Bichard (1964) worked on data from Leicester X Cheviot crosses and Suffolk crosses. They had two groups of ewes, one group having lambed at one year of age while the other group lambed at two years. In both groups, the effect of age of dam on the birth weight of the lamb was pronounced, mature ewes always giving heavier lambs than either one or two year old ewes. Type of birth was the major factor affecting birth weight, singles being 2.89 pounds heavier than twins. Males weighed .70 pounds more than females. In another set of data involving 4 years and analyzed within each year, males weighed between .42 and .97 pounds more than females and single lambs were between 1.49 and 2.21 pounds heavier than twins.

Sidwell _et_ _al_. (1964), in an extensive study of 4331 lambs from 4 breeds and breed crosses, used least square estimates to adjust the data for the different environmental differences. In their study the major sources that contributed to the variation between individuals were the main effects which included purebreds vs. crossbreds, sex, years, age of dam, and type of birth. Some of the more important interactions were also fitted in consecutive analyses. These included the interactions between sex X type of birth, sex X age of dam, sex X purebred or crossbred, type of birth X age of dam and sex X high or low year. All interactions were non-significant. Males were .51 pounds heavier than females, singles exceeded twins by 2.0 pounds and the age of dam effects were -.70, -.08, .41 and .39 for 2, 3, 4-6 and 7 or more years of age, respectively, with the last two groups not differing significantly. From their analysis of variance, all these main effects had significant influences on birth weight.

2. Weaning weight

Many workers have investigated the effects of various environmental factors on the weaning weight of lambs under either range or farm conditions. Donald and McLean (1935) in New Zealand, Bonsma (1939) in South Africa and Phillips and Dawson (1937, 1940) in Eastern United States, showed the importance of type of birth, sex, age of dam and birth weight on weaning weight and growth rate.

The most extensive and thorough work on this subject had been carried on by Hazel and Terrill (1945a, 1946a) on sheep raised under range conditions at the United States Department of Agriculture, Western Sheep Breeding Laboratory, Dubois, Idaho. Data on 2182 Rambouillet lambs were used to get the effects of the different environmental factors on weaning weight and staple length. Least squares estimates revealed that males were 8.3 pounds heavier than females, lambs from mature ewes weighed 6.1 pounds more than those of two-year old ewes, while single born lambs exceeded twins by 9.2 pounds and twins raised as singles by 2.5 pounds, respectively, all factors being significant. The regression of weaning weight on age in days was significant and was .413 pounds. Year and group differences did not contribute much to the variation in weaning weights and the interaction between factors was either non-significant or very small. Accordingly they concluded that these factors combine their effects additively, and were responsible for 50 percent of the total variation in weaning weights. In another study including 478 Columbia, 238 Corriedale and 366 Targhee lambs they found 10.8 and 8.7 pounds differences due to sex and age of dam, respectively. Single born lambs showed an excess of 11.7 and 5.1 pounds over twins and twins raised singly, and the regression was .448 pounds for weaning weight on age in days. All the factors were found to affect the weaning weight significantly and they contributed some 33 percent of the variation.

Sidwell and Grandstaff (1949), working with data on Navajo lambs, found that the reductions in the total sum of squares of weaning weight due to year of birth, age of dam, breed of sire, type of birth and weaning, sex and age of lamb at weaning were highly significant. Sex effect was 2.2 pounds in favor of males. For type of birth the effects were 4.7, -6.5 and 1.8 pounds for singles, twins and twins raised as singles, respectively. A preliminary analysis of the data revealed no difference in weaning weights of lambs from ewes 4 to 7 years old. The estimates for the age of dam effect were -1.80, 1.50, 1.70 and -1.40 pounds for 2, 3, 4-7 and 8 year old dams, respectively. The regression of weaning weight on age of lamb in days was .37 pounds.

Nelson and Venkatachalam (1949) showed in their analysis that significant portions of the total variation in weaning weight were due to sex, age of dam and type of birth, the latter having the major part. Karam _et al_. (1953) found that sex and type of birth have significant effects on weight of lambs at 155 days. Wethers weighed 3.0 pounds more than ewes and singles were 7.3 pounds heavier than twins. The regression of body weight on age in days estimated on a within year, flock, sire and type of birth was .27 pounds.

Blackwell and Henderson (1955) showed that years had a significant effect on weaning weight. There was an increase of 3.1 pounds for each increase of one year in the age of dam to a maximum of 5 years of age, the quadratic term being -.3 pounds. Sex difference was 3.3 pounds in favor of the males and singles were 5.4 pounds heavier than twins reared singly and 8.3 pounds heavier than twins. The regression of weaning weight on age of lamb in days was .1 pounds.

De Baca *et al*. (1956) investigated the factors that affect 120 day weight of crossbred spring lambs. They observed that there was an advantage of about 17 pounds for singles over twins and that wethers weighed 4.1 pounds more than ewe lambs. The interaction between sex and type of birth was non-significant. When the regression of 120 day weight on birth weight was added to the model, the difference between singles and twins dropped to 8.8 pounds, revealing that about half of the advantage singles have over twins is because of their original advantage in birth weight. The regression of 120 day weight on birth weight amounted to between 2.5 and 6.0 pounds for the different crosses in different years. Birth weight was very important in its effect on weaning weight. Birth type was the most influential factor on weaning weight.

MacNaughton (1956) found that Rambouillet females weighed 7.0 pounds less than males and 2.7 pounds less than wethers at weaning. Singles were 4.5 pounds heavier than twins raised singly and 14.7 pounds heavier than twins raised as twins. As for age of dam effect, he found that lambs from four to six year-old ewes exceeded those from two year-old ewes, three year-old ewes, and aged ewes by 8.5, 2.9, and 3.0 pounds respectively. The regression of weaning weight on age in days was .55 pound. In the Corriedale data the corresponding values were 5.5 and 2.0 pounds for sex effect, and 1.8 and 10.3 pounds for type of birth and rearing. Age of dam effects were 5.8, 2.6 and 3.2 pounds for the different age groups, respectively. The weight increased .47 pounds for each day of increase in the lamb's age.

Felts _et al_. (1957) studied data from 32 flocks in two consecutive years. Lambs weights were adjusted to 120 days of age and then constants were fitted within year and flock for the effects of age of dam and type of birth. Because a significant interaction between age of dam and type of birth was found in only 3 of the 74 flock-years, it was assumed to be unimportantly small or non-existent. Singles were about 10.0 pounds heavier than twins and 6.0 pounds heavier than twins raised as singles. Age of dam effects were -14.2, .1, 4.2, 4.6, 3.7, 2.0 and -.3 for dam ages from 1 year to 7 years, respectively.

Using the data from 3440 range Rambouillet lambs over a 25-year period, Shelton and Campbell (1962) found that male lambs were 4.67 pounds heavier than females and singles exceeded twins by 6.45 pounds and twins raised as singles by 2.96 pounds. Lambs from two year-old dams were significantly lighter than those from ewes 3 to 7 years of age, but were heavier than lambs from ewes over 8 years of age. The regression of weaning weight on age of lamb was .25 pounds per day.

Donald (1962) observed that the sex difference at weaning time was 7.0 pounds and that a difference of 14 pounds existed between singles and twins. Lambs from one year-old dams were 11 pounds less than those from two year-olds, the latter being 4 pounds less than lambs from mature ewes.

Balch (1962) found that year differences affected weaning weight significantly, with as much as 20 pounds difference between years. Type of birth and rearing had the most profound effect. Singles weighed 13.1 pounds more than twins and 5.3 pounds more than twins raised as singles. He also found a 4.2 pound difference between sexes in favor of males. Two year-old dams gave lambs that were lighter by 3.0, 5.6, 5.9, 4.2, 3.9 and 1.1 pounds than those from dams 3, 4, 5, 6, 7 and 8 years of age. Those from six, seven and eight year-old ewes did not differ significantly and lambs from nine-year-old dams were the lightest. The regression of 140 day weight on age was .192 pounds per day. All of these effects were highly significant.

Sidwell et al. (1964), working with 3423 lambs from four breeds and their crosses raised under farm conditions, found that weaning weight and gain from birth to weaning were both significantly affected by sex, type of birth and rearing, age of dam, age of lamb and the linear regression of weaning weight on birth weight. Also some of the interactions between the main effects were significant. They found that regression on birth weight was important and contributed significantly to the variation in weaning weight. Year differences were also evident for both traits. Males were 5.5 pounds heavier than females and singles exceeded twins by 11.5 pounds and twins raised singly by 5.3 pounds. Also twins raised singly exceeded twins by 6.2 pounds, the difference being significant. As for age of dam, the estimates they obtained were -2.2, 1.1, 1.8 and -.8 pounds for the 2, 3, 4-6 and 7+ years of age groups, with the middle ones not differing significantly.

Other workers investigating the same subject include Sidwell et al. (1956), Botkin et al. (1956), Warwick and Cartwright (1958), Harrington et al. (1958), Bennett and Knight (1962), Brothers and Whiteman (1962), Busch et al. (1962), Dalton (1962) and Yalcin and Bichard (1963). Their results were consistent with those already reported.

3. Yearling body weight

Phillips and Dawson (1940) observed that differences in body weight as a result of type of birth and age at weaning, which were important and significant in their effect on weaning weight, became less important at later ages. Singles were still heavier than twins in all groups at 12 months of age, but the difference was significant in only two of the six groups. As for regression on age, only 3 out of 12 regressions were significant compared with seven at 6 months of age. However, these differences were more pronounced as the lambs approached maturity.

Simmons (1943) found that the positive relationship between body weights at later ages were less in magnitude than at 3 months of age in the Karakul and mutton breeds.

Hazel and Terrill (1946c) observed that yearling Rambouillet ewes from mature dams were 2.6 pounds heavier than those from two year-old dams and single ewes weighed 6.0 and 0.5 pounds more than twins raised as twins and twins raised as singles, respectively, the differences being in the same direction as at weaning, but smaller. The regression of yearling body weight on age in days was .031 pounds as compared with .413 pounds at weaning time.

Terrill *et al*. (1947), working with Columbia and Targhee yearling ewes, found results that did not agree with those obtained by Hazel and Terrill (1946b). Singles were 7.1 and

2.4 pounds heavier than twins and twins raised singly in Columbia ewes, while the corresponding values for the Targhees were 4.7 and 7.4 pounds. Mature dams gave ewes 4.2 and .6 pounds more than those from two year-olds for the Columbia and Targhee, respectively, the latter being non-significant. The regressions of body weight on age at shearing were .186 and .296 pounds per day in the same order. Year differences were very important also. All the environmental effects accounted for 12 and 48 percent of the total variation in the Columbia and Targhee ewes respectively, which warrants adjusting the data for these factors.

In a study of New Zealand Romney Marsh sheep, Rae (1950) found that single born ewes exceeded twins by 6.6 pounds and twins raised singly by 2.2 pounds. Ewes from 3 year-old dams were 1.6 pounds heavier than those from 2 year-old dams and the regression of yearling body weight on age in days was .23 pounds.

Price _et_ _al_. (1953) investigated the effects of environmental factors on yearling traits of Navajo and Navajo crossbred ewes. The data included 917 yearling ewes retained from 1325 ewe lambs weaned in 13 breeding groups. Least square estimates showed that 48 percent of the total variation in body weight was due to breeding group. Mature dams gave ewes that were 3 pounds heavier than those from two year-old dams. Single ewes weighed 6.5 pounds more than twins and 1.5 pounds more than twins raised singly. The regression of body weight on age was .12 pounds per day.

Balch (1962) also found that differences due to year of birth, age of dam, type of birth, sex and regression on age in days contributed significantly to body weight at yearling age in sheep raised under farm conditions.

In a study including 1075 Navajo and Navajo crossbred yearling ewes Hall *et al*. (1964) found significant effects on body weight due to breeding group, type of birth and rearing, age of dam and regression of body weight on age at yearling. An interaction between breeding group and type of birth and rearing was non-significant. Also year differences contributed significantly to the total variation in body weight. The values they found for the contribution of each factor are discussed later.

4. Yearling fleece traits

An extensive study on the effects of some environmental factors on yearling fleece traits was conducted at the Western Sheep Breeding Laboratory, Dubois, Idaho, by Hazel and Terrill (1946c) on yearling Rambouillet ewes and by Terrill *et al*. (1947) on yearling Columbia and Targhee ewes. The traits they considered were staple length, grease fleece weight, body weight, body type, condition, face covering and neck folds. In addition, clean fleece weight was also considered for the yearling Rambouillet ewes. The environmental factors they studied were age of dam, type of birth and rearing, year of birth, age at shearing and percent inbreeding. In Rambouillets the staple length, grease fleece weight and clean fleece weight were significantly affected by type of birth and rearing. Single born ewes exceeded twins raised as twins and twins raised singly in yearling fleeces. Yearling ewes from mature dams had longer staple length and produced more wool than those from two year-old dams. Differences in the Columbia and Targhee breeds were in the same general direction. Yearly differences were the most important source of variation, followed by type of birth and rearing effects, age at shearing and percent inbreeding. Age of dam was the least important source of variation, but still contributed more than 2 percent of the variation in some cases.

The environmental factors studied accounted for 29, 29 and 33 percent of the total variation in grease fleece weight in the Rambouillets, Columbias and Targhees respectively and 21, 15 and 15 percent, respectively, of the total variability in staple length. In the rams of these three breeds the studies of Terrill et al. (1948a, 1948b) showed the same general trend of the effects of these environmental factors as was observed in the ewes, the magnitude being larger for grease and clean fleece weights and body weight, while it was somewhat less for staple length.

Rae (1950) investigated the effects of some environmental factors on New Zealand Romney Marsh yearling ewes. The effects of type of birth and rearing, age of dam, year of birth and age at shearing were of considerable magnitude in fleece weight, while they had a small or an opposite effect on staple length. In regard to his data, it must be stressed that the results presented refer to yearlings which were shorn as lambs at weaning. Twins and ewes from two year-old dams were able to overcome the handicap for staple length in the period between weaning and shearing. Thus maternal differences exert most of their effects prenatally and in the period between birth and weaning, where the milk production of the dam is the main source of nutrition for the lamb. However, differences due to type of birth and rearing and due to the age of dam effect still persisted for fleece weight and growth rate when the lambs were nine months old.

Also studying Romney Marsh and Corriedale hogget ewes, Wright and Stevens (1953) found a significant difference of .27 pounds between singles and twins in favor of the former for wool production.

Price _et al_. (1953), investigating the effects of some environmental factors on 917 yearling Navajo and Navajo crossbred ewes retained from 1325 ewe lambs weaned, found similar values. The traits they investigated were staple length, grease and clean fleece weight, body weight, body type and condition. Environmental effects accounted for a larger portion of the total variation in traits that are measurable than they accounted for in traits that are evaluated by scoring. The factors studied were breeding groups, age of dam, type of birth and rearing, years and age of ewe, which accounted for 47.7, 46.5, 37.5 and 47.8 percent of the total variation in staple length, grease fleece weight, clean fleece weight and body weight, respectively. All of the factors had significant effects on the measurable characters, breeding groups contributing the major part of the variation. Age of dam was also important for wool traits, followed by type of birth and rearing, age of ewe and years, in this order.

Turner (1961) found that the clean wool weight differed between the handicapped and unhandicapped animals. Mature dams gave ewes that exceeded ewes from two year-old dams by $.30 \pm .11$ pounds in clean wool weight, while the difference between rams was $.30 \pm .17$ pounds for the same effect. Single ewes and single lambs exceeded twin ewes and twin rams by $.30 \pm .12$ and $.48 \pm .15$ pounds for the same trait.

In farm raised sheep, Balch (1962) found that environmental factors caused considerable variation in body traits and more in fleece traits. He investigated the effects of year of birth, age of dam, type of birth and rearing, sex and age of animal at shearing. The factors studied had a significant effect on grease fleece weight and staple length, except for age of dam on staple length which was of sizable magnitude, but lacked significance. Rams had .4 cm shorter staple than ewes, which is a reversal of the findings of Terrill et al. (1948a). He also stated that the contribution of these environmental effects for each trait to the total variability were large enough to warrant correction for these factors.

Hall et al. (1964), using 1075 yearling Navajo and Navajo crossbred ewes grouped in 3 breeding groups, studied the effects of year of birth, breeding group, type of birth and rearing, age of dam and the regression on age in days at shearing. All of the factors had a significant effect on the measurable wool traits; i.e. grease and clean fleece weight, fiber diameter and staple length, except for age of dam on both staple length and fiber diameter, and type of birth and rearing and regression on age in fiber diameter. The interaction between breeding group and type of birth and rearing had no significant effects on any of the characters they investigated except body condition. The Navajo ewes were generally lighter in weight and had smaller grease and clean fleece weights. Group C had the longest staple length and heaviest clean fleece weight. Singles generally exceeded twins and twins raised as singles in all traits. Both body and fleece traits increased or improved with increasing age of dam up to 4 to 6 years of age and then declined slightly. Breeding group and year of birth accounted for the major portion of the variation in staple length and fiber diameter.

B. Heritability

The total phenotypic variance of a trait in a population σ_p^2 can be partitioned as

$$\sigma_p^2 = \sigma_H^2 + \sigma_E^2 + \sigma_{EH}^2$$

where: σ_H^2 is the variance due to hereditary differences between individuals in the population, and σ_E^2 is the variance due to temporary and permanent environmental effects, and σ_{EH}^2 is the variance due to the interaction between heredity and environmental effects.

The variance due to differences in heredity of individuals which treats each genotype as an integral unit, can be further subdivided into three descriptive parts as follows:

$$\sigma_H^2 = \sigma_G^2 + \sigma_D^2 + \sigma_I^2$$

σ_G^2 is the variance due to the additive effects of genes in the population, and

σ_D^2 is the variance due to interaction between allelic genes, usually known as the variance due to dominance, and

σ_I^2 is the variance due to interaction between non-allelic genes, usually referred to as the epistatic variance.

Lush (1948) gave two definitions for the heritability of a character in a population. The ratio between $\frac{\sigma_H^2}{\sigma_P^2}$ is known as heritability in the broad sense, measuring the fraction of the variance due to all gene effects, whether manifested consistently or only in combination with certain other genes that influence a trait. The other definition is the ratio $\frac{\sigma_G^2}{\sigma_P^2}$, i.e. heritability in the narrow sense, which measures the fraction of the variance due to the additive or average effects of the genes. The non-additive effects of dominance and epistasis do not contribute much to permanent change in a population, if ordinary systems of mating are the prevailing practice. In this case the additive genetic portion of variance and hence heritability in the narrow sense, is important in determining the improvement achieved by mass selection. On the other hand, where matings are planned in order to benefit from the nicking ability of certain developed strain crosses, the variance due to dominance and epistasis becomes more important. In more prolific species the use of such planned matings may be practiced successfully. With less prolific species the practice of developing certain strains and testing them for combining ability is more difficult.

Methods of estimating heritability are based on the extent to which related individuals resemble each other more than individuals drawn at random from a given population. These estimates usually contain certain amounts of the non-additive effects of genes in addition to all the additive part, depending on the particular method of estimation used.

Many estimates of heritability of different traits in sheep have been reported by various workers, and are presented in Table 1.

The heritability estimates of body weight at different ages tend to be of moderate or medium high values except some individual low values like the estimate of .07 obtained by Blackwell and Henderson (1955) for weaning weight, the high estimates for birth weight of .72 reported by Nelson and Venkatachalam and the Warwick and Cartwright estimate of .77 for weaning weight. The heritability estimates of wool traits found in the literature indicate that they are fairly highly heritable characters. Staple length, fiber diameter and clean fleece weight seem to be less affected by environmental differences than body weights. Surplus energy is deposited as protein or fat, and can act as a reservoir in times of environmental stress so that wool fiber growth tends to proceed along its genetically determined course. Clean fleece weight is more highly hereditary than grease fleece

Table 1. Estimates of heritability of some production traits in sheep

Estimate	Breed	Remarks	Reference
Birth weight			
.15	Average of 5 breeds	504 dam-offspring pairs	Nelson and Venkatachalam (1949)
.72	Average of 5 breeds	Paternal half-sibs correlation	Nelson and Venkatachalam (1949)
.19	3 breeds and crosses	1956 paternal half-sibs	Ali (1952)
.54	3 breeds and crosses	766 dam-offspring pairs	Ali (1952)
.34	Ossimi	218 dam-offspring pairs	Ragab *et al*. (1953)
.18	Karakul	728 paternal half-sibs	Yao *et al*. (1953)
.35	Karakul	207 dam-offspring pairs	Yao *et al*. (1953)
.25	Karakul	Regression on mid-parent	Yao *et al*. (1953)
.33	4 breeds	1632 dam-offspring pairs	Blackwell and Henderson (1955)
.09	Suffolk	Regression of offspring on dam	Cassard and Weir (1956)
.27	Rambouillet	2282 dam-offspring pairs	MacNaughton (1956)
.36	Corriedale	1586 dam-offspring pairs	MacNaughton (1956)
.21	Welsh Mountain sheep	Regression of offspring on dam	Dalton (1962)
.54	Columbia X Rambouillet	1785 paternal half-sibs	Eloksh *et al*. (1962)

Table 1. (Continued)

Estimate	Breed	Remarks	Reference
-.14		717 dam-offspring pairs	Butcher and Welsh (1964)
.10		Paternal half-sibs correlation	Butcher and Welsh (1962)
<u>Weaning weight</u>			
.27	Rambouillet	2183 paternal half-sibs	Hazel and Terrill (1945)
.34	Rambouillet	892 dam-offspring pairs	Hazel and Terrill (1945)
.17	Columbia, Corriedale, and Targhee	Average of two methods	Hazel and Terrill (1946)
.29	Average of 5 breeds	348 dam-offspring pairs	Nelson and Venkatachalam (1949)
.42	Average of 5 breeds	Paternal half-sibs correlation	Nelson and Venkatachalam (1949)
.14	Shropshire	890 paternal half-sibs	Ali (1952)
.38	Shropshire	395 dam-offspring pairs	Ali (1952)
.34		593 paternal half-sibs	Karam <u>et al</u>. (1953)
.10	Ossimi	202 dam-offspring pairs	Ragab <u>et al</u>. (1953)
.14	Rambouillet, Targhee and Columbia rams	Paternal half-sibs correlation	Kyle and Terrill (1953)

Table 1. (Continued)

Estimate	Breed	Remarks	Reference
.11	Rambouillet, Targhee and Columbia ewes	Paternal half-sibs correlation	Kyle and Terrill (1953)
.21	Navajo crossbreds	646 dam-offspring pairs	Sidwell (1954)
.07	4 breeds	784 dam-offspring pairs	Blackwell and Henderson (1955)
.41	Suffolk	Regression of offspring on dam	Cassard and Weir (1956)
.33	Rambouillet	1003 dam-offspring pairs	MacNaughton (1956)
.45	Corriedale	815 dam-offspring pairs	MacNaughton (1956)
.41		Regression on mid-parent	Warwick and Cartwright (1957)
.27		Regression on sire performance	Warwick and Cartwright (1957)
.77		1405 dam-offspring pairs	Warwick and Cartwright (1957)
.15		Paternal half-sibs correlation	Felts et al. (1957)
.22	Rambouillet	Regression of offspring on dam	Shelton (1959)
.07	Hampshire	498 paternal half-sibs	Givens et al. (1960)
.51	Welsh Mountain sheep	Regression of offspring on dam	Dalton (1962)

Table 1. (Continued)

Estimate	Breed	Remarks	Reference
.19	Rambouillet	Regression of offspring on dam	Shelton and Campbell (1962)
.30	Rambouillet	3440 paternal half-sibs	Shelton and Campbell (1962)
.14	Columbia and Southdale	Paternal half-sibs correlation	Balch (1962)
.12	Hampshire X Rambouillet crosses	Paternal half-sibs correlation	Carter and McClure (1962)
.08	Hampshire X Rambouillet crosses	Regression of progeny mean on sire record	Carter and McClure (1962)
.21	Columbia and Corriedale	707 paternal half-sibs	Botkin (1964)
.59	Columbia and Corriedale	Full-sib correlation	Botkin (1964)
<u>Yearling body weight</u>			
.40	Rambouillet	1622 dam-offspring pairs	Terrill and Hazel (1943)
.36	Australian Merino	Regression of offspring on dam	Morley (1951)
.21	Australian Merino	Paternal half-sibs correlation	Morley (1951)
.21	Rambouillet, Targhee and Columbia rams	Paternal half-sibs correlation	Kyle and Terrill (1953)
.40	Rambouillet, Targhee and Columbia ewes	Paternal half-sibs correlation	Kyle and Terrill (1953)

Table 1. (Continued)

Estimate	Breed	Remarks	Reference
.09	Australian Merino	Paternal half-sibs correlation	Morley (1955)
.36	Australian Merino	Regression of offspring on dam	Morley (1955)
.52	Rambouillet	514 dam-offspring pairs	MacNaughton (1956)
.46	Corriedale	185 dam-offspring pairs	MacNaughton (1956)
.64	Australian Merino ewes	Regression of offspring on dam	Young *et al*. (1960)
.53	Australian Merino rams	Regression of offspring on dam	Young *et al*. (1960)
.13	Columbia and Southdale	Paternal half-sibs correlation	Balch (1962)
.36	Navajo and Navajo crossbred ewes	867 dam-offspring pairs	Hall *et al*. (1964)
Grease fleece weight			
.40	Rambouillet	70 dam-offspring pairs	Rasmussen (1942)
.24	Corriedale	173 dam-offspring pairs	Rasmussen (1942)
.28	Rambouillet	1622 dam-offspring pairs	Terrill and Hazel (1943)
.10 to .15	New Zealand Romney	Extensive data	McMahon (1943)
.10 to .15	New Zealand Romney	200 dam-offspring pairs	Rae (1948)

Table 1. (Continued)

Estimate	Breed	Remarks	Reference
.40	Mixed breeds	233 dam-offspring pairs	Cockerham (1949)
.17	New Zealand Romney	640 degrees of freedom for dam-offspring	Rae (1950)
.39	Australian Merino	529 degrees of freedom for dam-offspring	Morley (1951)
.67	Australian Merino	459 paternal half-sibs	Morley (1951)
.27	3 breeds and crosses	1624 paternal half-sibs	Ali (1952)
.51	3 breeds and crosses	315 dam-offspring pairs	Ali (1952)
.14	Rambouillet, Targhee and Columbia rams	Paternal half-sibs correlation	Kyle and Terrill (1953)
.49	Rambouillet, Targhee and Columbia ewes	Paternal half-sibs correlation	Kyle and Terrill (1953)
.53	Romney Marsh and Corriedale	Regression of offspring on dam	Wright and Stevens (1953)
.40	Australian Merino	Regression of offspring on dam	Morley (1955)
.44	Australian Merino	Paternal half-sibs correlation	Morley (1955)
.42	4 breeds	538 dam-offspring pairs	Blackwell and Henderson (1955)

Table 1. (Continued)

Estimate	Breed	Remarks	Reference
.39		Paternal half-sibs correlation	Felts *et al*. (1957)
.29	New Zealand and Romney	Regression of offspring on dam	Rae (1958)
.45	Australian Merino ewes	Regression of offspring on dam	Young *et al*. (1960)
.33	Australian Merino rams	Regression of offspring on dam	Young *et al*. (1960)
.58	Welsh Mountain sheep	Regression of offspring on dam	Dalton (1962)
.69	Columbia and Southdale	Paternal half-sibs correlation	Balch (1962)
.34	Navajo and Navajo crossbred ewes	867 dam-offspring pairs	Hall *et al*. (1964)
Clean fleece weight			
.38	Rambouillet	310 dam-offspring pairs	Terrill and Hazel (1943)
.62	Australian Merino	135 degrees of freedom for dam-offspring	Morley (1951)
.20	Rambouillet, Targhee and Columbia ewes	Paternal half-sibs correlation	Kyle and Terrill (1953)
.47	Australian Merino	Regression of offspring on dam	Morley (1955)
.26	Australian Merino	Paternal half-sibs correlation	Morley (1955)

Table 1. (Continued)

Estimate	Breed	Remarks	Reference
.45	Australian Merino ewes	Regression of offspring on dam	Young *et al*. (1960)
.29	Australian Merino rams	Regression of offspring on dam	Young *et al*. (1960)
.19	Navajo and Navajo crossbred ewes	867 dam-offspring pairs	Hall *et al*. (1964)
Staple length			
.36	Rambouillet	1622 dam-offspring pairs	Terrill and Hazel (1943)
.21	New Zealand Romney	200 dam-offspring pairs	Rae (1948)
.35	New Zealand Romney	640 dam-offspring pairs	Rae (1950)
.22	Australian Merino	107 degrees of freedom for dam-offspring	Morley (1951)
.24	Australian Merino	459 Paternal half-sibs	Morley (1951)
.27	Rambouillet, Targhee and Columbia rams	Paternal half-sibs correlation	Kyle and Terrill (1953)
.42	Rambouillet, Targhee and Columbia ewes	Paternal half-sib correlation	Kyle and Terrill (1953)
.56	Australian Merino	Regression of offspring on dam	Morley (1955)

Table 1. (Continued)

Estimate	Breed	Remarks	Reference
.52	Australian Merino	Paternal half-sibs correlation	Morley (1955)
.35	New Zealand Romney	Regressiong of offspring on dam	Rae (1958)
.37	Australian Merino ewes	Regression of offspring on dam	Young *et al*. (1960)
.31	Australian Merino rams	Regression of offspring on dam	Young *et al*. (1960)
.38	Welsh Mountain sheep	Regression of offspring on dam	Dalton (1962)
.73	Columbia and Southdale	Paternal half-sibs correlation	Balch (1962)
.23	Navajo and Navajo crossbred ewes	867 dam-offspring pairs	Hall *et al*. (1964)
Fiber diameter			
.33	Rambouillet, Targhee and Columbia rams	Paternal half-sibs correlation	Kyle and Terrill (1953)
.37	Rambouillet, Targhee and Columbia ewes	Paternal half-sibs correlation	Kyle and Terrill (1953)
.30	Navajo crossbreds	646 dam-offspring pairs	Sidwell (1954)
.45	Australian Merino ewes	Regression of offspring on dam	Young *et al*. (1960)

Table 1. (Continued)

Estimate	Breed	Remarks	Reference
.37	Australian Merino rams	Regression of offspring on dam	Young et al. (1960)
.35	Navajo and Navajo crossbred ewes	867 dam-offspring pairs	Hall et al. (1964)

weight because the latter is influenced by variations in yolk deposition, dirt, and plant fibers, as well as by clean fleece weight.

1. Phenotypic correlations

Reasonably accurate estimates of correlation coefficients among traits are useful if maximum efficiency from selection is to be attained. This is true because it is seldom that only one trait is selected for improvement at a given time. Hazel (1943) states that, "A knowledge of the phenotypic correlations among productive traits is essential for the construction of selection indexes designed to maximize the rate of genetic improvement". Rae (1950) looks at it from yet another point of view as he states that it is possible and sometimes desirable to use an easily recognized and measurable trait or combination thereof, to predict the magnitude of another trait which may be more difficult and more expensive to measure.

The literature contains several estimates of correlations among various traits on the same animal. These include the relationships between body weight at different stages, others include the correlations among wool traits and components, and still others include those observed between body weights and wool traits. Table 2 shows some of the phenotypic correlations between a number of economically important characters in sheep, especially those raised under range conditions.

The correlation between body weight at different ages is quite high. This is expected because of the part-whole relationship and because both the environmental and genetic factors that affect weight at an earlier stage have a carry-over effect on weight at a subsequent age. The environmental effects would include those effects due to the mothering ability and the milk production of its dam, and also the amount of nutrition available to the animal. Genes that have a pleiotropic effect on weight would tend to increase the genetic contribution to the phenotypic correlation.

Moderately positive relationships have been shown to exist between body weight at shearing age and fleece weight. The maternal and nutritional effects on body weight may also

Table 2. Phenotypic correlations between some of the production traits in sheep

Traits considered	Estimate	Reference
Birth weight and weaning weight	.40	MacNaughton (1956)
Birth weight and weaning weight	.52	MacNaughton (1956)
Birth weight and weaning weight	.57	Galal (1961)
Birth weight and weaning weight	.32	Butcher et al. (1964)
Birth weight and weaning weight	.60	Shelton (1964)
Birth weight and shearling weight	.36	MacNaughton (1956)
Birth weight and shearling weight	.37	MacNaughton (1956)
Birth weight and yearling weight	.50	Galal (1961)
Birth weight and yearling weight	.48	Shelton (1964)
Weaning weight and shearling weight	.46	MacNaughton (1956)
Weaning weight and shearling weight	.61	MacNaughton (1956)
Weaning weight and shearling weight	.75	Galal (1961)
Weaning weight and shearling weight	.65	Shelton (1964)
Grease fleece weight and clean fleece weight	.80	Jones et al. (1944)
Grease fleece weight and clean fleece weight	.77	Morley (1950)
Grease fleece weight and clean fleece weight	.72	Terrill et al. (1950)
Grease fleece weight and clean fleece weight	.66 to .75	Kyle and Terrill (1953)
Grease fleece weight and clean fleece weight	.80 to .88	Terrill and Kyle (1953)
Grease fleece weight and clean fleece weight	.81	Sidwell et al. (1956)
Grease fleece weight and clean fleece weight	.72 to .92	Price et al. (1964)
Grease fleece weight and staple length	.22 to .42	Pohle and Keller (1943)
Grease fleece weight and staple length	.24	Jones et al. (1944)
Grease fleece weight and staple length	.22	Morley (1950)
Grease fleece weight and staple length	.45	Rae (1950)
Grease fleece weight and staple length	.24 to .47	Terrill and Kyle (1953)
Grease fleece weight and staple length	.21 to .34	Hall et al. (1964)

Table 2. (Continued)

Traits considered	Estimate	Reference
Grease fleece weight and fiber diameter	.03	Jones et al. (1944)
Grease fleece weight and fiber diameter	.15	Morley (1950)
Grease fleece weight and fiber diameter	.24 to .45	Terrill and Kyle (1953)
Grease fleece weight and fiber diameter	.06 to .14	Hall et al. (1964)
Clean fleece weight and staple length	.56	Jones et al. (1944)
Clean fleece weight and staple length	.48	Morley (1950)
Clean fleece weight and staple length	.55	Terrill et al. (1950)
Clean fleece weight and staple length	.43 to .60	Terrill and Kyle (1953)
Clean fleece weight and staple length	.62	Sidwell et al. (1956)
Clean fleece weight and staple length	.59	Shelton (1959)
Clean fleece weight and staple length	.18 to .58	Price et al. (1964)
Clean fleece weight and staple length	.33	Hall et al. (1964)
Clean fleece weight and fiber diameter	.14	Morley (1950)
Clean fleece weight and fiber diameter	.19 to .49	Terrill and Kyle (1953)
Clean fleece weight and fiber diameter	.09	Shelton (1964)
Clean fleece weight and fiber diameter	.14 to .21	Hall et al. (1964)
Staple length and fiber diameter	-.11	Jones et al. (1944)
Staple length and fiber diameter	.03	Morley (1950)
Staple length and fiber diameter	.07 to .49	Terrill and Kyle (1953)
Staple length and fiber diameter	.19 to .23	Hall et al. (1964)
Weaning weight and grease fleece weight	.46 to .58	Terrill and Kyle (1953)
Weaning weight and clean fleece weight	.30	Shelton (1964)
Weaning weight and staple length	.15	Terrill et al. (1950)
Weaning weight and staple length	.11	Ercanbrack (1952)
Weaning weight and staple length	.14	Karam et al. (1953)

Table 2. (Continued)

Traits considered	Estimate	Reference
Weaning weight and staple length	.02	Sidwell (1955)
Weaning weight and fiber diameter	-.01 to .12	Terrill and Kyle (1953)
Weaning weight and fiber diameter	-.18	Shelton (1964)
Yearling weight and grease fleece weight	.30 to .52	Pohle and Keller (1943)
Yearling weight and grease fleece weight	.26	Jones et al. (1944)
Yearling weight and grease fleece weight	.30	Morley (1950)
Yearling weight and grease fleece weight	.04	O'Ferrall and Vial (1962)
Yearling weight and grease fleece weight	.22 to .26	Hall et al. (1964)
Yearling weight and clean fleece weight	.30 to .42	Pohle and Keller (1943)
Yearling weight and clean fleece weight	.26	Jones et al. (1944)
Yearling weight and clean fleece weight	.25	Morley (1950)
Yearling weight and clean fleece weight	.16 to .19	Hall et al. (1964)
Yearling weight and clean fleece weight	.12 to .50	Price et al. (1964)
Yearling weight and clean fleece weight	.38	Shelton (1964)
Yearling weight and staple length	.12 to .16	Pohle and Keller (1943)
Yearling weight and staple length	-.02	Jones et al. (1944)
Yearling weight and staple length	.12	Morley (1950
Yearling weight and staple length	-.03 to .03	Hall et al. (1964)
Yearling weight and fiber diameter	.02	Jones et al. (1944)
Yearling weight and fiber diameter	.15	Morley (1950)
Yearling weight and fiber diameter	.05 to .10	Hall et al. (1964)
Yearling weight and fiber diameter	.05	Shelton (1964)

have an effect, in the same direction, on wool production in the same animal. The correlation between wool traits reported in the literature tends to be of high or moderate magnitude, depending on the traits involved. For example, grease fleece weight and clean fleece weight are almost always found to be moderately strongly related. Clean fleece weight seems also to be highly correlated with staple length and to a lesser extent with fiber diameter. Thus a reasonably accurate prediction of clean fleece weight can be obtained from the other wool traits, mainly grease fleece weight and staple length. This possibility has been investigated extensively by many workers because of the difficulty of measuring clean fleece weight directly.

2. Genetic correlations

The phenotypic correlation between two characters is not a reliable estimate of the genetic relationship existing between them. This is a consequence of the phenotypic correlation being measured on the same animal where the environments affecting them are certain to be closely correlated and likely to make an important contribution to their phenotypic relationship.

Lush (1948) has stated the most important causes of genetic correlations between traits. Firstly, genes which affect one trait also affects the other, usually known as pleiotropy. This could be due to a gene producing two or more substances each of which affects a different trait, or to only one primary gene effect which starts a chain of consequences that later affect two or more traits. This mode of action need not necessarily be in a given direction. It could affect both traits in the same direction, or it could affect them in opposite ways. Secondly, linkage could be a cause of genetic correlations especially if the population is derived from a recent cross between divergent strains or breeds, or if the population is really composed of non-interbreeding groups, but analyzed as if it were a single population. Linkage is usually a minor cause because crossing over in a freely interbreeding population tends to equalize the frequency of coupling and repulsion double heterozygotes, except in cases where linkage has been very close and not many generations have elapsed between the first crosses and the analyzed population. Lastly, if selection has been strong for one trait and weak for the other in a segment of the population, while the reverse has happened in another segment, this would tend to create a genetic correlation between the traits. Of these three causes, pleiotropy is the most important one in many characteristics studied in domesticated animals.

The means of estimating genetic correlations between traits have been explained by Hazel (1943) where the possibility of correlated environments has been overcome by correlating trait X on one individual with trait Y in a close relative. The closer the relationship between the two individuals, without introducing environmental correlations, the more accurate the measurement will be. The formula introduced for that is

$$r_{G_1 G_2} = \frac{\sqrt{(\mathrm{Cov}\ X_1\ Y_2) \cdot (\mathrm{Cov}\ X_2\ Y_1)}}{\sqrt{(\mathrm{Cov}\ X_1\ X_2) \cdot (\mathrm{Cov}\ Y_1\ Y_2)}}$$

where the subscripts 1 and 2 indicate two related individuals.

Thus a genetic correlation is, to a large extent, a measure of the relationship between the additive deviations caused by genes in the two traits. Statistically, the characters considered may be envisaged as having some multivariate distribution of additively genetic values, which requires for its specification, the array of genetic variances and covariances. As the genetic correlations are expressed in a standardized form, they are consequently preferred to genetic covariances for interpretation and comparisons.

Table 3 shows some of the reported genetic correlations existing between important wool and body traits in sheep.

Table 3. Genetic correlations between some of the production traits in sheep

Traits considered	Estimate	Reference
Birth weight and weaning weight	1.04	Ragab *et al.* (1953)
Birth weight and weaning weight	.24	MacNaughton (1956)
Birth weight and weaning weight	.54	MacNaughton (1956)
Birth weight and shearling weight	.44	MacNaughton (1956)
Birth weight and shearling weight	.51	MacNaughton (1956)
Weaning weight and shearling weight	.06	MacNaughton (1956)
Weaning weight and shearling weight	.06	MacNaughton (1956)
Weaning weight and shearling weight	.18	Balch (1962)
Grease fleece weight and clean fleece weight	.72	Morley (1950)
Grease fleece weight and clean fleece weight	.93	Hall *et al.* (1964)
Grease fleece weight and staple length	.25	Rae (1950)
Grease fleece weight and staple length	.60	Rae (1950)
Grease fleece weight and staple length	-.39	Morley (1950)
Grease fleece weight and staple length	.37	Balch (1962)
Grease fleece weight and staple length	.08	Hall *et al.* (1964)
Grease fleece weight and fiber diameter	-.10	Hall *et al.* (1964)
Clean fleece weight and staple length	-.38	Morley (1950)
Clean fleece weight and staple length	.44	Hall *et al.* (1964)
Clean fleece weight and fiber diameter	.01	Hall *et al.* (1964)
Staple length and fiber diameter	.36	Sidwell (1955)
Staple length and fiber diameter	.15	Hall *et al.* (1964)
Weaning weight and staple length	-.17	Karam *et al.* (1953)
Weaning weight and staple length	-.10	Sidwell (1955)
Weaning weight and staple length	.52	Balch (1962)

Table 3. (Continued)

Traits considered	Estimate	Reference
Weaning weight and fiber diameter	1.19	Sidwell (1955)
Yearling weight and grease fleece weight	.15	Morley (1950)
Yearling weight and grease fleece weight	-.07	Hall *et al.* (1964)
Yearling weight and clean fleece weight	-.06	Morley (1950)
Yearling weight and clean fleece weight	-.05	Hall *et al.* (1964)
Yearling weight and staple length	-1.11	Morley (1950)
Yearling weight and staple length	-.24	Hall *et al.* (1964)
Yearling weight and fiber diameter	-.16	Hall *et al.* (1964)

III. SOURCE OF DATA

A. Description of Breeding Flock

The data used in this study are the births, and weanling body weights and the yearling body and wool traits, obtained from records of the Navajo and Navajo crossbred sheep produced and maintained at the Southwestern Range and Sheep Breeding Laboratory, Fort Wingate, New Mexico.

The origin of the Navajo sheep has been reported by Blunn (1940, 1943) and by Sidwell (1949, 1954). The Navajo sheep are descendants of the first sheep brought to what is now the United States. At present some 73,000 Navajo Indians along with their 355,000 sheep live on a reservation which comprises an area of nearly 16,000,000 acres located in northwestern New Mexico, northeastern Arizona and that portion of Utah south of the San Juan River. This reservation is in a semi-arid region, with sparse desert vegetation at the lower elevations. This has been depleted by over grazing, resulting in accelerated erosion. About 400 years of natural selection has resulted under these conditions in a very hardy sheep and ewes that are excellent mothers. The sheep tend to have narrow bodies, long legs and little wool on their faces. Their fleece consists of a long coarse outer coat and a short fine under coat containing much kemp and other medullated fibers.

A study was started in 1934 by the officials of the Bureau of Indian Affairs, U.S. Department of the Interior and the Bureau of Animal Industry, U.S. Department of Agriculture. They found that the need of the people on the reservation, from the sheep standpoint, was to improve both the quality and quantity of wool obtained from these sheep, with the necessity of preserving their hardy characteristics. The income derived from wool and lamb sold through marketing channels has been the principal means of subsistence of the Navajo people for many generations. In addition it provides them with meat for home consumption and wool for hand weaving. Rug weaving earlier required from 15 to 20 percent of the wool produced. This necessitated that wool quality be uniform and free from kemp and other medullated fibers. The best wool for this purpose was of quarter blood grade. Since the remaining 80 percent of the wool is sold off the reservation on a commercial basis, it was desirable to develop another strain that has wool of a finer grade, in order to compete with other wool in the market. According to these needs three research projects have been conducted at the Southwestern Range and Sheep Breeding Laboratory.

1. <u>Research Project I</u>

This was directed towards improving the "old type" Navajo sheep by linebreeding and selection within the Navajo strain. The Laboratory maintains a group of the old type Navajo sheep to study the effect of selection in this strain. These are derived from the original foundation flock of some 800 ewes and 20 rams which were obtained from more remote areas of the Navajo reservation where the influence of the improved breeds was less likely to be found. With improvement in wool quality and mutton conformation, the Navajo strain could provide a valuable means of transporting their hardiness qualities to other breeds by crossbreeding. The selection of rams was based largely on quality and quantity of wool, body type, and freedom from fleece impurities, while for the yearling ewes selection was against kemp and hairy fleeces. As for lambs, the greatest emphasis, at culling time, was placed on weaning weight, staple length, and condition score.

2. Research Project II

The objective of this project is to develop a fine wool sheep suited to the semi-arid conditions of this southwestern area, and especially on the Indian reservation. Emphasis is placed on staple length, grade, freedom from kemp and medullated fibers, adaptability, and lamb production. As a result of selecting for the above traits, it is hoped to develop an animal that will survive successfully and produce maximum wool, of a suitable quality for commercial use, and produce lambs that will meet the requirements for feed lot operations. The combination of these should provide a maximum return on sheep investments, especially with the ever-decreasing amount of hand weaving practiced by the Navajo people.

The fine-wool strain has been developed from the original matings of Targhee rams to ewes with fine wool selected from a crossbred group. The crossbred group has been developed according to the following chart.

Corriedale X Navajo   Romney X Navajo

(½ Corriedale, ½ Navajo)   (½ Romney, ½ Navajo)

(½ Navajo, ¼ Corriedale, ¼ Romney)

crossbred ewe group

Since 1954 the fine wool line has been closed to outside blood and the matings were made <u>inter</u> <u>se</u>. Lamb selection was based on weaning weight and more emphasis has been placed on wool traits in this line than in the other lines.

3. <u>Research Project III</u>

The purpose of this project is to develop a coarse-wool sheep that will produce wool suitable for the needs of the Navajo Indian and lambs that could be used in the feedlots. As mentioned above, a portion of the wool grown is used in hand weaving rugs and blankets. This wool should be in a grade range of 46 to 58's spinning count, this being the most suitable range for hand weaving. The production of the above quality wool on an animal adapted to the existing environment is of utmost importance to the Navajo Indian living on the reservation. With this in mind, selection has been placed primarily on those animals displaying hardiness, body size, good staple length, and high clean wool production.

As the fleeces of the crossbred ewes mentioned above were too fine for hand weaving operations, it was thought advisable to introduce rams of Lincoln and Cotswold breeding in order to produce wool with a lower spinning count. By that time the amount of Navajo blood in the resulting cross had been much diluted, and their desired characteristics were in danger of being lost. Additional crosses of Navajo and Columbia and Navajo and Romney were performed, which in turn were reciprocally mated to the Lincoln and Cotswold cross progeny. As with the case of the fine wool line, the coarse wool line has been closed since 1954 and matings were performed *inter se*.

B. Management Practices

As the main object of the Southwestern Range and Sheep Breeding Laboratory was to improve wool and mutton quality of the sheep in the hands of the Navajo Indians on the reservation, the experimental herd was maintained strictly under range conditions similar to those found on the reservation where the seed stock was purchased and where the improved breeding stock will be used. Only during breeding and lambing time were the ewes and rams kept in corrals at the Laboratory site, where they were fed on alfalfa hay. Also during the early stpring in dry years it was necessary to start feeding alfalfa pellets.

Body weights, scores, and wool clip were taken on all rams, yearlings and two-year-old ewes in April of every year. Traits scored were: face covering, outer-coat, color, horns, jaw formation, and belly covering. A lock of wool was clipped from the side of each animal to measure the staple length to the nearest 1 mm. Cross sections were made to measure the average fiber diameter, using the Hardy thin cross-section device and the rapid count method (Hardy and Wolf, 1939). Shearing was usually done in April and a small side sample was obtained from each fleece. Grease fleece weight was obtained at shearing time by weighing individual fleeces to the nearest 0.1 pound. Clean fleece weight was estimated prior to 1958 by scouring small side samples (Schott _et al_., 1942), which proved to be highly correlated with the weight obtained by scouring the whole fleeces and is much less expensive. Beginning in 1958 and in later years, clean fleece weight was estimated by use of the Neale Squeeze Machine (Neale _et al_., 1956). In 1956 this machine was tried on a sample of 595 fleeces of the fine wool and coarse wool lines, and was found sufficiently accurate for estimating clean fleece weight. Correlations between clean fleece weight and machine reading, grease fleece weight and machine reading, and between actual scoured whole fleece and grease fleece weight were .94, .83 and .76 respectively, with better results with the coarse wool fleeces.

Lambing usually took place immediately after shearing in late April and during the month of May. In order to identify each lamb permanently a metal ear tag was placed in each ear a few hours after the lamb was born. At that time the ear tag number, date of birth, sex, birth weight to the nearest 0.05 pound, and any abnormality or other pertinent observation was recorded. The lambs were weaned early in September of each year at approximately 120 days of age, at which time the weaning weight to the nearest pound, staple length and body scores were recorded. Lamb culling took place in October and was based on measurements and scores taken at weaning time. Also mature ewes were culled at that time, largely on their physical appearance. The lambs and ewes that were culled were sold. In December, the ewes and rams were weighed, branded, and assigned to breeding pens. They usually stayed there for 31 days and the ewes were trucked back to the range in early January where they stay until April. The rams remained on a fenced range near the laboratory site.

C. The Observations

The data used in this study include lambs that were born over a period of 12 years from 1950 through 1961 inclusive. These lambs were from the three breeding groups (or lines) mentioned previously. They are referred to as the Navajo group (N), the fine wool group (F), and the coarse wool group (C).

The traits included in this study represent two lamb traits which are birth weight and weaning weight and five yearling traits which are body weight, grease fleece weight, clean fleece weight, staple length, and mean fiber diameter, measured as have been mentioned.

The birth and weanling weights were measured on a total of 3264 lambs. At weaning time the lambs were usually separated from their mothers some hours before weighing. The yearling traits were measured on a total of 1221 ewes and 413 rams. As they were born in May, and shearing took place during the last part of the following April, the wool shorn represents that produced in approximately 365 days. Body weights were taken during June when the sheep were around 400 days of age. The weight was recorded to the nearest pound.

All individuals with unknown parentage have been excluded from the data, as well as those individuals when any of the environmental effects studied were not complete. Lambs that were born but did not survive till weaning time were also dropped from this investigation. It was thought advisable not to include them, because birth weight by itself has no great economic importance except as it indicates body traits at subsequent stages of life. Triplets, which were too few to consider as a category by themselves, were included with lambs that were born twins. The number of individuals used to estimate the genetic parameters was slightly less than those given above as a result of excluding rams with only one offspring in a given year, and are shown in Table 4 with the number of sires used grouped by year and breeding group for lambs studied for the weanling traits. The number of sires shown in the table is larger than the actual number because some of the sires were used in more than one year. This was a common practice in the earlier years of this investigation.

Table 4. Number of lambs and their sires studied for weanling traits grouped by year and breeding group

Year	Lines: F Number of lambs	F Number of sires	N Number of lambs	N Number of sires	C Number of lambs	C Number of sires	Totals Number of lambs	Totals Number of sires
1950	32	6	24	3	171	25	227	34
1951	16	5	11	3	35	9	62	17
1952	82	8	53	4	247	17	382	29
1953	64	4	49	5	146	11	259	20
1954	81	6	70	5	173	12	324	23
1955	59	4	64	4	121	7	244	15
1956	79	4	81	3	130	6	290	13
1957	77	3	77	3	72	3	226	9
1958	72	3	103	3	74	3	249	9
1959	91	4	126	3	105	4	322	11
1960	112	3	111	3	117	4	340	10
1961	136	4	114	4	78	4	328	12
Total	901	54	883	43	1469	105	3253	202

IV. METHODS OF ANALYSIS

A. Estimation of Environmental Effects

Selection of genetically superior individuals to be the parents of the next generation is hampered by environmental factors that tend to mask the actual breeding values of the parents. The contribution of these environmental effects to the total phenotypic variation should be eliminated before proceeding with the analysis of the data. This can be achieved either by including these factors simultaneously in the mathematical model, thus eliminating that part of the total variance attributed to their influence, or by identifying, measuring and correcting the data according to their estimated effects. In the case of a balanced or proportional set of data the two procedures mentioned give the same final result. If disproportionality of subclass numbers exists, the first method gives cleaner estimates of genetic parameters sought, since it tends to eliminate bias due to inequalities within a factor not included in the model, e.g. inequality of sex representation within a given sire or sires, which could happen merely by chance. However, in the present investigation, it was important to evaluate the effects of the different environmental factors that affect different traits, and it was not possible to include all factors investigated in the same model because of the enormous size of the resulting matrix that needs to be inverted. A possible solution for this was to absorb a certain factor or factors within another factor in the set up model then turn around and set up another model where the absorbed factor (s) would be represented while absorbing another set. This would require solving more than one model, according to the number of factors absorbed, and would increase enormously the time and expense of computation. Due to the facts presented above, it was decided to use the second procedure to obtain the estimates sought from the data.

The method of analysis used in this study is the least squares method suggested by Yates (1934) and extended by Hazel (1946) and Henderson (1948) to include the covariance between the dependent variable and an independent continuous variable. This method is resorted to when disproportionality of subclass frequencies causes non-orthogonality between different effects, as is the case in this study. This method consists of fitting constants for each of the independent variables which in this case are the measurable environmental effects that are included in the mathematical model.

1. The mathematical model

The choice of a mathematical model that defines a population from which the observations are considered a sample, rests more or less on the knowledge of the biological factors involved in determination of the traits studied. One could concieve of many environmental and genetic effects that could be important. However, a compromise should be sought to render a model that is simple enough to be solved, and yet represents as completely as possible the biology behind the situation. For example, a linear model may not be the best representative of the way factors involved are combined, but its simplicity in solving and statistical treatment makes it the best suited for study.

The following additive model was adopted as satisfactory for representing the weaning weight of a lamb

$$Y_{ijklmn} = u + r_i + b_j + a_k + t_l + s_m + d\ X_{ijklmn} + e_{ijklmn}$$

where

Y_{ijklmn} is the weaning weight of the nth lamb in the ith year in the jth breeding group and kth age of dam class and the lth type of birth and rearing and of the mth sex.

In this model weaning weight is expressed as the sum of the effects in the classification part of the model plus an effect due to regression of weight on age at weaning plus all effects peculiar to this lamb. The last term includes all environmental and genetic effects not specified in the model.

Effects that are common to all individuals in the population are included in the constant, u. It is caused by certain things that are shared by all animals, such as belonging to the same species, and having certain morphological and physiological characteristics in common. Environmental effects which are the same for all animals, such as general health and managerial procedures are included in this constant. Restrictions placed on the other parameters in the model define its composition and imply that u is the mean of the parent population in which equal subclass frequencies existed.

The r_i is an effect common to all individuals born in the ith year. It includes differences between years that are caused by environmental conditions peculiar to each year such as variations in annual rainfall, temperature, supply and quality of food, changes in location of grazing range and prevalence of parasites and other unidentifiable factors. Changes in average genetic merit of individuals from year to year are also included in the year effect.

The b_j factor is common to all individuals belonging to the jth breeding group, where b_1, b_2 and b_3 refers to the Fine-wool, Navajo, and Coarse-wool breeding groups, respectively. As mentioned before, the breeding groups were developed towards different goals so the differences between them could be mostly genetic.

The a_k includes effects which are common to all animals with the kth age of dam. The age of dam classifications represented here are a_1 (two year-old dam), a_2 (three year-old dams), a_3 (four to seven year-old dams), and a_4 (eight year-old and older dams). In a_3 dams of ages 4, 5, 6, and 7 were grouped together since it was thought that individuals born from dams of these ages differ little from each other. This has been shown by previous work by Sidwell (1949) and Hall et al. (1964). The effect of age of dam on the weight of individuals is largely due to the difference in milking ability of dams belonging to different ages. It is the general experience that two year-old dams have a lower milk supply than older dams and the very oldewes are usually poorer mothers than younger dams. Some genetical differences between dams in their maternal ability may be included in this effect.

The t is the effect which the lth classification for type of birth has on the observations. The three types of birth and rearing represented in this study are

t_1 Lambs born and reared singly

t_2 Lambs born and reared as twins

t_3 Twin lambs reared as singles

The type of birth effect is due to the fact that twins share uterine space and nourishment, and they also have to share their dam's milk supply after birth. Accordingly they may have an initial handicap as compared with single lambs.

The s_m is an effect common to all individuals belonging to the mth sex. This represents the difference between the weights of male and female offspring.

The linear regression coefficient of weight on age of the nth individual (d) is analogous to the daily gain made by the lambs around weaning time.

X_{ijklmn} is the deviation of the age of nth animal of the ijklm subclass from 120 days of age at weaning. The error, eijklmn, is the difference between the actual observation and the sum of all effects included in the model. This discrepancy is due to environmental factors not included in the model, to the effects that the sire and dam may have on different offspring, to dominance and epistatic effects and to chance in Mendelian sampling.

A second model was also fitted for weaning weight which is the same as the first model with the addition of a factor CO_{ijklmn} where C is the linear regression coefficient measuring the average change in weaning weight for an increase of one pound in birth weight, and, O_{ijklmn} is the deviation of the birth weight of the nth animal in the ijklm subclass, from the mean birth weight of all animals in the study.

The above mentioned two models were used in the analysis of weaning weight. The same model is used for birth weight with minor changes. These are

a. The regression of weight on age does not exist.

b. The type of birth effect t only include the first two subclasses i.e. t_1 and t_2, since there is no differentiation of rearing practice at birth.

The models fitted for the yearling traits are the same as that used for weaning weight with the following substitutions

a. Yearling body weight: A term for the regression of weight on age at yearling is substituted for that at weaning. In this case X_{ijklmn} becomes the deviation of the age of the nth animal of the ijklm subclass from the 400 days of age at yearling.

b. Yearling wool traits: A term for the regression of each of the four traits; grease fleece weight, clean fleece weight, staple length, and mean fiber diameter on age at shearing is included in the same model above. However, X_{ijklmn}, in this case, is the deviation of the age of the nth animal from the 365 days of age at shearing.

2. <u>The least squares equations and conditions</u>

A set of equations is obtained from this analysis one representing each of the factors included and the mean. These equations are

$$\hat{\mu}: \quad n_{.....}\mu + \sum_i n_{i....}r_i + \sum_j n_{.j...}b_j + \sum_k n_{..k..}a_k +$$

$$\sum_l n_{...l.}\, t_l + \sum_m n_{....m}s_m + d\, X_{.....} = Y_{.....}$$

$$\hat{r}_i:\ n_{i\cdots\cdot}\mu + n_{i\cdots\cdot}r_i + \sum_j n_{ij\cdots}b_j + \sum_k n_{i\cdot k\cdot\cdot}\, a_k +$$

$$\sum_l n_{i\cdot\cdot l\cdot}\, t_l + \sum_m n_{i\cdot\cdot\cdot m}\, s_m + d\, X_{i\cdots\cdot\cdot} = Y_{i\cdots\cdot\cdot}$$

$$\hat{b}_j:\ n_{\cdot j\cdots}\mu + \sum_j n_{ij\cdots}\, r_i + n_{\cdot j\cdots}b_j + \sum_k n_{\cdot jk\cdot\cdot}\, a_k + \sum_l n_{\cdot j\cdot l\cdot}t_l$$

$$+ \sum_m n_{\cdot j\cdot\cdot m}\, s_m + d\, X_{\cdot j\cdots\cdot} = Y_{\cdot j\cdots\cdot}$$

$$\hat{a}_k:\ n_{\cdot\cdot k\cdot\cdot}\mu + \sum_i n_{i\cdot k\cdot\cdot}r_i + \sum_j n_{\cdot jk\cdot\cdot}b \ + n_{\cdot\cdot k\cdot\cdot}\, a_k +$$

$$\sum_l n_{\cdot\cdot kl\cdot}\, t_l + \sum_m n_{\cdot\cdot k\cdot m}\, s_m + d\, X_{\cdot\cdot k\cdot\cdot\cdot} = Y_{\cdot\cdot k\cdot\cdot\cdot}$$

$$\hat{t}_l:\ n_{\cdot\cdot\cdot l\cdot}\mu + \sum_i n_{i\cdot\cdot l\cdot}\, r_i + \sum_j n_{\cdot j\cdot l\cdot}\, b_j + \sum_k n_{\cdot\cdot kl\cdot}\, a_k +$$

$$n_{\cdot\cdot\cdot l\cdot}\, t_l + \sum_m n_{\cdot\cdot\cdot lm}\, s_m + d\, X_{\cdot\cdot\cdot l\cdot\cdot} = Y_{\cdot\cdot\cdot l\cdot\cdot}$$

$$\hat{s}_m:\ n_{\cdot\cdot\cdot\cdot m}\mu + \sum_i n_{i\cdot\cdot\cdot m}\, r_i + \sum_j n_{\cdot j\cdot\cdot m}\, b_j + \sum_k n_{\cdot\cdot k\cdot m}a_k +$$

$$\sum_l n_{\cdot\cdot\cdot lm}\, t_l + n_{\cdot\cdot\cdot\cdot m}\, s_m + d\, X_{\cdot\cdot\cdot\cdot m\cdot} = Y_{\cdot\cdot\cdot\cdot m\cdot}$$

$$\hat{d}:\ X_{\cdot\cdot\cdot\cdot\cdot}\mu + \sum_i X_{i\cdots\cdot}\, r_i + \sum_j X_{\cdot j\cdots}b_j + \sum_k X_{\cdot\cdot k\cdot\cdot}\, a_k +$$

$$\sum_l X_{\cdot\cdot\cdot l\cdot}\, t_l + \sum_m X_{\cdot\cdot\cdot\cdot m}\, s_m + \sum_{i,\,j,\,k,\,l,\,m,\,n} X^2_{ijklmn} =$$

$$\sum_{i,\,j,\,k,\,l,\,m,\,n} X_{ijklmn}\, Y_{ijklmn}$$

where the (.) denotes summation over corresponding subscript. As could be seen from the above equations, the sum of the coefficients for the estimates of the different factors denoted by (^) is equal to the coefficient of the mean in the $\hat{\mu}$ equation, i.e. $\sum_i n_{i....} = n.....$ Also, the sum of the coefficients of one factor in another factor's equation is equal to the coefficient of the latter factor, e.g. $\sum_j n_{ij...} = n_{i....}$ and the total of the RHS's of the $\hat{r}_i$, b_j,......, d is equal to Y....., the grand total. Accordingly, a solution cannot be possible until restrictions (or constraints) are imposed. These restrictions imposed are

$$\sum_i \hat{r}_i = \sum_j \hat{b}_j = \sum_k \hat{a}_k = \sum_l \hat{t}_l = \sum_m \hat{S}_m = 0$$

Any other set of restrictions could have been used and will give the same results, but this was preferred for easier computation. As for the error term e_{ijklmn}, it has the same assumptions required for the analysis of variance, and described by Eisenhart (1947). These specify that if the errors (e's) have a mean equal to zero and a constant variance σ_e^2, and are uncorrelated with each other, then the estimates derived are unbiased, and if the model is truly additive then they are the "best" estimates. If tests of significance are to be entirely valid the distribution of the errors must be normal.

B. Estimation of Heritability

1. Paternal half-sib correlation

In a random mating population the heritability of a given trait could be estimated from the analysis of variance of observations represented by a hierarchal classification. Therefore, an observation on a certain animal could be assumed to be the sum of effects of a factor tested within another, and so on, such as

$$Y_{ijk} = \mu + g_i + s_{ij} + e_{ijk}$$

where

μ is the general mean, g_i is the effect due to the ith year-breeding group subclass, s_{ij} is the effect of the jth sire in ith year-breeding group, and e_{ijk} is the error associated with the kth individual in the ijth subclass, and resulting from the difference between the observed value and the effects included in the model. In this model it is assumed that the g_i are fixed effects whose sum is zero. Other assumptions concerning this model are

a) $E\ (s_{ij}) = E\ (e_{ijk}) = 0$
b) $E\ (s^2_{ij}) = \sigma^2_s$ and $E(e^2_{ijk}) = \sigma^2_e$
c) that all the elements in the model are uncorrelated.

If these assumptions hold then we have, where $k \neq k'$

$E[(Y_{ijk} - \mu_i) \quad (Y_{ijk'} - \mu_i)] = \sigma_s^2$, the covariance between half-sibs, and

$$E(Y_{ijk} - \mu_i)^2 = \sigma_s^2 + \sigma_e^2$$

is the variance of individual phenotypic values within year-breeding group subclasses. It is assumed that the environmental deviations (e's) are randomly associated with the genotypes and the non-environmental part of an individual phenotype is determined only by his genotype, and not through other effects such as maternal effects. In random mating populations the covariance between half-sibs, estimated by σ_s^2, the sire component of variance, is an estimate of $1/4\ \sigma_G^2 + 1/16\ \sigma_{GG}^2$ + etc. where σ_G^2 is the additive variance, and σ_{GG}^2 + etc. are the additive X additive, and so on, genetic variances or what is known as the epistatic variance. To the extent that epistatic variance is non-existent, and the dams are unrelated to each other or to the sire, the ratio

$$\frac{4\hat{\sigma}_s^2}{\hat{\sigma}_s^2 + \hat{\sigma}_e^2} \text{ is a consistent estimate of heritability}$$

in the "narrow sense", defined by Lush (1940). The bias introduced by assuming no epistatic variance will be small in random mating populations and this situation applies to the present data since the analysis was done within breeding groups. Whatever bias is introduced will increase the numerator of the above ratio by only 1/4 of the two-gene interactions and 1/16 of the three-gene interactions, etc., and these are likely to be small as compared with the sampling errors.

The sampling variance of the intraclass correlation,

$$\hat{t} = \frac{\hat{\sigma}_s^2}{\hat{\sigma}_s^2 + \hat{\sigma}_e^2}$$

is given by Robertson (1959) as

$$V(\hat{t}) = \frac{2(1-t)^2\,[1+(n-1)t]^2}{n(n-1)(s-1)},$$

where s is the number of sire groups, and n is the number of offspring per sire. When n varies, the quantity,

$$n_o = \frac{1}{s-1}\left[N - \frac{\sum_i n_i^2}{N}\right],$$ is substituted for n.

However, one can get a more accurate estimate of the variance of (t) and consequently of the heritability estimate than is obtained by following the procedure indicated above.

In a two-way hierarchal classification the analysis of variance is as follows

Source of variation	Degrees of freedom	Sum of squares	Expected sum of squares	Expected mean squares
Between sires	s-1	S	$[N- \frac{\sum_i n_i^2}{N}]\sigma_s^2+\sigma_e^2(s-1)$	$\sigma_e^2 + n_o\ \sigma_s^2$
Within sires	N-s	E	$\sigma_e^2\ (N-s)$	σ_e^2

Let $Q = \frac{\hat{\sigma}_s^2}{\hat{\sigma}_e^2}$, and express the intraclass correlation in the form $t = \frac{Q}{1 + Q}$

The variance of a ratio $Z = \frac{X}{Y}$, neglecting powers of the ratio greater than the first, is

$$\text{Var }(Z) = Z^2 \left[\frac{\text{Var }(X)}{X^2} \quad \frac{\text{Var }(Y)}{Y^2} \quad \frac{2\text{ Cov }(X,Y)}{XY}\right]$$

Accordingly

$$\text{Var }(t) = t^2 \left[\frac{\text{Var }(Q)}{Q^2} \quad \frac{\text{Var }(1+Q)}{(1+Q)^2} \quad \frac{2\text{ Cov}[Q,\ (1+Q)]}{Q\ (1+Q)}\right].$$

Since Var (1+Q) = Var (Q), and Cov [Q, (1+Q)] = Var (Q),

$$\text{Var }(t) = t^2 \left[\frac{\text{Var }(Q)}{Q^2} \quad \frac{\text{Var }(Q)}{(1+Q)^2} \quad \frac{2\text{ Var }(Q)}{q\ (1+Q)}\right]$$

$$= t^2 \left[\frac{\text{Var }(Q)\ [(1+Q)^2 + Q^2 - 2Q\ (1+Q)]}{Q^2\ (1+Q)^2}\right]$$

$$= t^2 \left[\frac{\text{Var }(Q)}{Q^2\ (1+Q)^2}\right]$$

$$= \left[\frac{Q}{1+Q}\right]^2 \left[\frac{\text{Var }(Q)}{Q^2\ (1+Q)^2}\right]$$

$$= \frac{\text{Var }(Q)}{(1+Q)^4} \tag{1}$$

The variance of (t) now is in terms of the variance of the Q quantity which is defined as $\frac{\hat{\sigma}_s^2}{\hat{\sigma}_e^2}$, and its variance is that of the ratio,

$$\text{Var }(Q) = \text{Var}\left[\frac{\hat{\sigma}_s^2}{\hat{\sigma}_e^2}\right]$$

$$= \left[\frac{\hat{\sigma}_s^2}{\hat{\sigma}_e^2}\right]^2 \left[\frac{\text{Var }(\hat{\sigma}_s^2)}{(\hat{\sigma}_s^2)^2} + \frac{\text{Var }(\hat{\sigma}_e^2)}{(\hat{\sigma}_e^2)^2} - \frac{2\text{ Cov }(\hat{\sigma}_s^2,\ \hat{\sigma}_e^2)}{(\hat{\sigma}_e^2)\ (\hat{\sigma}_s^2)}\right]$$

Since Eisenhart (1947) has pointed out that mean squares are uncorrelated then

$$\text{Cov }(E,\ S) = \text{Cov }(\hat{\sigma}_e^2,\ \hat{\sigma}_e^2 + n_o\ \hat{\sigma}_s^2) = 0$$

$$\text{or Var}\ (\hat{\sigma}_e^2) + n_o \text{ Cov}\ (\hat{\sigma}_e^2, \hat{\sigma}_s^2) = 0$$

then

$$\text{Cov}\ (\hat{\sigma}_e^2, \hat{\sigma}_s^2) = -\frac{V\ (\hat{\sigma}_e^2)}{n_o}, \text{ and}$$

$$\text{Var}\ (Q) = Q^2 \left[\frac{\text{Var}\ (\hat{\sigma}_s^2)}{(\hat{\sigma}_s^2)^2} + \frac{\text{Var}\ (\hat{\sigma}_e^2)}{(\hat{\sigma}_e^2)^2} + \frac{2\ \text{Var}\ (\hat{\sigma}_e^2)}{n_o(\hat{\sigma}_e^2)(\hat{\sigma}_s^2)}\right]$$

$$= Q^2 \left[\frac{\text{Var}\ (\hat{\sigma}_s^2)}{(\hat{\sigma}_s^2)^2} + \frac{\text{Var}\ (\hat{\sigma}_e^2)}{(\hat{\sigma}_e^2)^2} \left[1 + \frac{2\ \hat{\sigma}_e^2}{n_o \hat{\sigma}_s^2}\right]\right]$$

$$= Q^2 \left[\frac{\text{Var}\ (\hat{\sigma}_s^2)}{(\hat{\sigma}_s^2)^2} + \frac{\text{Var}\ (\hat{\sigma}_e^2)}{(\hat{\sigma}_e^2)^2} \left[1 + \frac{2}{n_o} \frac{1}{Q}\right]\right]$$

Since it is known that

$$\text{Var}\ (\hat{\sigma}_e^2) = \frac{2\ \hat{\sigma}_e^4}{N-s}$$

$$\text{Var}\ (Q) = Q^2 \left[\frac{\text{Var}\ (\hat{\sigma}_s^2)}{(\hat{\sigma}_s^2)^2} \quad \frac{2\ \hat{\sigma}_e^4}{(N-s)\hat{\sigma}_e^4} \left[1 + \frac{2}{n_o} \frac{1}{Q}\right]\right]$$

$$= Q^2 \left[\frac{\text{Var}\ (\hat{\sigma}_s^2)}{\hat{\sigma}_s^4} \quad \frac{2}{N-s} \left(1 + \frac{2}{n_o} \frac{1}{Q}\right)\right] \qquad (2)$$

The last term in (2) will be very small where the value of N-S is large, unless n_o the average number of offspring per sire is very small or N-s is very small or both are small. If this term is dropped, then

$$\text{Var (Q)} = Q^2 \left[\frac{\text{Var }(\hat{\sigma}_s^2)}{\hat{\sigma}_s^4}\right]$$

$$= \left[\frac{\hat{\sigma}_s^2}{\hat{\sigma}_e^2}\right]^2 \left[\frac{\text{Var }(\hat{\sigma}_s^2)}{\hat{\sigma}_s^4}\right]$$

$$= \frac{\hat{\sigma}_s^4}{\hat{\sigma}_e^4} \cdot \frac{\text{Var }(\hat{\sigma}_s^2)}{\hat{\sigma}_s^4}$$

$$= \frac{\text{Var }(\hat{\sigma}_s^2)}{\hat{\sigma}_e^4} \qquad (3)$$

Now, if we substitute the value for the variance of (Q) obtained from (3) in Equation (1) we get that

$$\text{Var (t)} = \frac{\text{Var }(\hat{\sigma}_s^2)}{\hat{\sigma}_e^4} \left[\frac{1}{(1+Q)^4}\right]$$

$$= \frac{\text{Var }(\hat{\sigma}_s^2)}{\hat{\sigma}_e^4} \cdot \frac{1}{\left[1 + \frac{\hat{\sigma}_s^2}{\hat{\sigma}_e^2}\right]}$$

$$= \frac{\text{Var }(\hat{\sigma}_s^2)}{(\hat{\sigma}_e^2)^2} \cdot \frac{(\hat{\sigma}_e^2)^4}{(\hat{\sigma}_e^2 + \hat{\sigma}_s^2)^4}$$

$$= \frac{\text{Var }(\hat{\sigma}_s^2) \cdot \hat{\sigma}_e^4}{(\hat{\sigma}_e^2 + \hat{\sigma}_s^2)^4} \qquad (4)$$

It is seen from (4) that all quantities needed are available from the analysis of variance table except the variance component between sires (or groups), i.e. Var $(\hat{\sigma}_s^2)$. This has been developed by many workers in the case of equal subclass numbers (Osborne and Patterson, 1952).

In the case of the unbalanced arrangement it becomes more complex than in the balanced case. The complexity arises from the fact that although the mean squares between groups and within groups are independent from one another, the mean square between groups is not distributed as χ^2 any longer (except if $\hat{\sigma}_s^2 = 0$), but the mean square within groups is still distributed as a χ^2, with N-s degrees of freedom.

Crump (1951) gave the variance of the variance component between groups for the case of a one-way classification or

$$\text{Var }(\hat{\sigma}_s^2) = \frac{2\sigma_e^4}{n_o^2}\left[\frac{1}{(s-1)^2}\left[\left(\frac{1}{N}\sum_i \frac{n_i^2}{w_i}\right)^2 + \sum_i \frac{n_i^2}{w_i^2} - \frac{2}{N}\sum \frac{n_i^3}{w_i^2}\right] + \frac{1}{N-s}\right] \qquad (5)$$

where $w_i = \dfrac{n_i}{1 + n_{iQ}}$, with Q having the same value as before.

If in formula (5) the bracketed quantity is designated as C , then

$$\text{Var }(t) = \frac{2\ \hat{\sigma}_e^4}{n_o^2}\,[C]\,\frac{\hat{\sigma}_e^4}{(\hat{\sigma}_e^2 + \hat{\sigma}_s^2)^4}$$

$$= \frac{2}{n_o^2}\,[C]\frac{(\hat{\sigma}_e^2)^4}{(\hat{\sigma}_e^2 + \hat{\sigma}_s^2)^4} \;\cdot$$

$$= \frac{2}{n_o^2}\,[C]\;\left[\frac{(\hat{\sigma}_e^2)^4}{(\hat{\sigma}_e^2)^4}\;\left[\frac{\hat{\sigma}_e^2}{\hat{\sigma}_e^2} + \frac{\hat{\sigma}_s^2}{\hat{\sigma}_e^2}\right]^{-4}\right]$$

$$= \frac{2}{n_o^2}\,[C]\;\left[\frac{1}{(1+Q)^4}\right] \qquad (6)$$

The last term in the quantity [C] in formula (5), $\frac{1}{N-s}$, will have a very small value and could be easily dropped, unless N is very small, and s the number of sires is large. Since

$$n_o^2 = \frac{1}{(s-1)^2}\left[N - \frac{\sum\limits_i n_i^2}{N}\right]^2 ,$$

in the [C] term the quantity $\frac{1}{(s-1)^2}$ can be canceled from both numerator and denominator.

Since in (5),

$$w_i = \frac{n_i}{1 + n_i Q},$$

then $\dfrac{n_i}{w_i} = 1 + n_i Q$;

$$\frac{n_i^2}{w_i^2} = (1 + n_i Q)^2;$$

$$\frac{n_i^2}{w_i} = (1 + n_i Q)\, n_i ,$$

and $\dfrac{n_i^3}{w_i^2} = (1 + n_i Q)^2 n_i$

If we substitute these values in [C] and hence in formula (6) the variance of (t) is

$$\text{Var (t)} = \frac{2}{(1+Q)^4 n_o^2} \cdot \frac{1}{(s-1)^2}$$

$$\left[\left[\frac{1}{N} \sum_i (1 + n_i Q) n_i\right]^2 + \sum_i (1 + n_i Q)^2 - \frac{2}{N} \sum_i (1 + n_i Q)^2 n_i \right]$$

For the present data, the standard error of heritability estimates is 4 times that of the intraclass correlation. When applied to the birth weights in this study, the standard error from this formula is smaller than that obtained from the usual method by 43 percent. I think that it will give the same or similar results if applied to the rest of the traits investigated in this study.

2. Intra-sire regression of offspring on dam

Whenever a sire is mated to several females, the regression of offspring on mid-parent provides an unsuitable estimate of heritability. This arises as a consequence of the correlation between mid-parent values when the sire is represented more than once. In cases where the number of dams far exceeds the number of sires, the simple regression on either parent is unsuitable for estimating heritability. In these cases, the most logical estimate of heritability can be made from the regression of offspring on dam within sire groups.

The intra-sire regression of offspring on dam, as Lush (1940) pointed out, dodges most of the environmental correlations between offspring and parents because the dams which are mated to the same sire and their offspring are usually kept under the same management. Many of these group differences, some of which may be genetic, are eliminated with sire differences, and hence do not contribute to the covariance term. A large part of any possible time trend is eliminated in this way, but an additional precaution for overcoming time trends is that of performing the analysis on an intra-sire and intra-year basis. Since the three breeding groups represented in this study were selected for different purposes and no interbreeding between them was allowed, it is expected that they might have differed by the time the study was carried out, and consequently the data were analyzed also on an intra-breeding group basis. It was also thought that, since the record of the dam and those of her offspring were obtained in different years, there might exist an effect due to the year of dam being good or bad from the environmental point of view. Accordingly, the data used for calculating the heritability from the regression of offspring on dam were analyzed on an intra year of dam, sire, year of offspring, and breeding-group basis.

It should be noted also, that this method estimates the heritability as the genic fraction of the phenotypic variance which actually did occur among individuals mated to the same sire, thus circumventing for the most part the problems about departures from random mating.

The most important advantage of this method is that it is not biased by the selection of dams, as the covariance between dam and offspring is reduced to the same extent as the variance of the dams, so that the slope of the regression line is unaltered (Falconer, 1960). This holds true where the parents were selected only on their phenotypic performance in the trait whose heritability is being estimated. Any selection that is based on anything else except the phenotype of the parent for that trait could cause a bias in the resulting estimate. If selection was practiced for other traits, i.e. like selection based on an index including some other characters, the regression will not be biased if the traits included were independent of the trait studied. This of course is not always true because the previously selected traits may in fact have positive or negative genetic correlations with the trait of primary immediate interest.

In this study, the parents must have been selected on weaning weight previously. At yearling time they may have been selected also on a combination of body and wool traits that are measured at that time. Lush (1940) also states that selection of the offspring of course would impair the validity of any estimate of heritability based on them. Should this be the case, the estimate of heritability will be too low, since selection will tend to reduce the covariance between parent and offspring, while the variance of offspring record does not enter in the regression estimate.

The estimates of heritability thus obtained will contain the desired additively genetic portion of the phenotypic variance, with a slight amount of the variance due to epistatic effects. On the average dominance deviations will be cancelled since dominance deviations do not contribute to the resemblance between parent and offspring within sires. Dominance will bias the estimates obtained from this method to the extent that resemblance between parent and offspring is between a parent and twin offsprings. The dams that have twin offspring in a given year will be represented twice in computing heritability, consequently will tend to bias the estimate downwards. Kempthorne and Tandon (1953) have pointed out that the procedure of computing the regression by repeating the parent's record with each offspring's record would be valid if the correlation among offspring of a parent were zero. The method of averaging the offsprings' records would be valid if the correlations between them were unity. However, they found that in the case of milk production in dairy cattle only a small difference could be detected between estimates of heritability calculated by repeating the dam's record with each daughter's record, using a weighted regression, or using an unweighted regression of means of daughters on their dams. In their data they had 28.6 percent of dams that had more than one daughter. Accordingly, they attributed the existence of a small difference between the three methods of estimation to the fact that a large proportion of the records was from dams with only one offspring, and because the correlation between records of offspring from the same parent was very small. Thus, in this investigation the record of the dam was repeated with each of her offspring records to get the pertinent covariances.

The standard errors of the regression coefficients were obtained following the procedure outlined by Snedecor (1956). The regression coefficient and its standard error when doubled will yield both the heritability estimate and its standard error.

C. Genetic Correlations

The regression of offspring record for one trait on the record of the dam for another trait appeared suitable for evaluating the genetic correlations between different traits. From the same analysis which was used for calculating the heritability of different traits, it was also possible to obtain the regressions and covariances of different traits on both the dam and offspring. These resulting covariances were used to obtain estimates of the genetic correlations from the formula mentioned in II-D, thus reducing the amount of computations needed. Two covariances were obtained for each two traits studied, resulting in 42 covariances between the seven traits measured on both dam and offspring.

D. Phenotypic Correlations

The phenotypic correlations between traits studied were obtained from the adjusted data. The analysis of variance procedure was used for obtaining these correlations, by summing each two characters and obtaining both the variance of the sums and of the individual traits. According to the following formula for the variance of a sum, it was possible to obtain the covariance between each of two traits that enter in a particular sum from

$$\mathrm{Var}\ (X + Y) = \mathrm{Var}\ (X) + \mathrm{Var}\ (Y) + 2\ \mathrm{Cov}\ (XY)$$

then;

$$\mathrm{Cov}\ (X, Y) = 1/2\ [\mathrm{Var}\ (X + Y) - \mathrm{Var}\ (X) - \mathrm{Var}\ (Y)]$$

In this case the number of degrees of freedom for the respective variances and covariances was determined by the number of individuals having both traits represented.

The analysis was performed, as for estimates of heritability and genetic correlations, within year of birth of dam, sire, year of offspring, and breeding-group.

V. RESULTS

A. Effects of Environmental Factors on Production Traits

There were two reasons for evaluating the effects of some environmental factors on production traits of the sheep in this study. The first purpose was to measure how much these different factors influence the traits studied. The second purpose was to use this information to adjust the data for the important effects prior to estimating genetic parameters. The magnitude of the effects of these factors differs from one trait to another depending on the susceptibility of the trait to the variation in environmental conditions. Accordingly, the contribution of the fixed environmental factors on each character is being reported separately.

1. Birth weight

The mean, standard deviation, and estimates of the fixed environmental effects for birth weight obtained from the least squares analysis, are presented in Table 5. The mean birth weight of all 3264 individuals studied was 8.03 pounds. Year of birth was an important source of variation, which fluctuated about the general mean, essentially at random. Table 6 shows the mean squares for the different environmental effects and the residual mean square, obtained from

Table 5. Means, standard deviations, and least squares estimates of environmental factors for birth and weaning weights

Classification	Number of lambs	Birth weight (lbs.)		Weaning weight (lbs.)	
		Estimate	Standard error	Estimate	Standard error
Mean	3264	8.03		53.31	
Residual standard deviation		1.21		8.05	
Years:					
1950	248	- .08	.08	-10.23	.52
1951	78	- .38	.13	-17.23	.86
1952	384	- .30	.06	+ 9.10	.42
1953	260	+ .25	.07	+ 0.46	.49
1954	324	- .19	.07	- 0.81	.44
1955	244	- .56	.08	- 5.25	.50
1956	291	+ .05	.07	+ 2.93	.46
1957	226	- .33	.08	+ 5.87	.52
1958	249	- .33	.08	- 3.05	.50
1959	291	+ .06	.07	- 0.63	.47
1960	340	+ .95	.07	+11.09	.43
1961	329	+ .87	.07	+ 7.74	.46
Type of birth and rearing:					
Single	2430	+ .84	.03	+ 6.65	.27
Twin	671	- .84	.03	- 7.24	.31
Twin raised as single	163	--	--	+ 0.59	.37

Table 5. (Continued)

Classification	Number	Birth weight (lbs.)		Weaning weight (lbs.)	
		Estimate	Standard error	Estimate	Standard error
Age of dam:					
2 years	813	- .88	.06	- 4.85	.37
3 years	725	- .21	.06	+ 0.63	.37
4 - 7 years	1670	+ .28	.05	+ 2.40	.33
8 years or more	56	+ .81	.13	+ 1.82	.26
Sex:					
Ram	1367	+ .23	.02	+ 2.57	.15
Ewe	1897	- .23	.02	- 2.57	.15
Breeding group:					
N	886	- 1.14	.03	- 3.31	.22
C	1454	+ .48	.03	+ 1.48	.20
F	924	+ .66	.03	+ 1.83	.21
Regression on age in days		--	--	+ 0.381	.019
R^2		.495		0.610	

Table 6. Mean squares of birth weight and weaning weight obtained from least squares analysis

Source of variation	Degrees of freedom	Birth weight[a]	d.f.	Weaning weight[a]
Between years	11	34.4**	11	13096.9**
Between breeding groups	2	867.6**	2	7311.9**
Between types of birth and rearing	1	1561.6**	2	45781.4**
Between ages of dam	3	237.5**	3	8821.5**
Between sexes	1	148.6**	1	18971.3**
Between ages of lamb	--	--	1	27367.7**
Residual	3245	1.464	3243	64.81
Total	3263		3263	

[a]In this table and the following tables
** means significant at the .01 level
* means significant at the .05 level.

the least squares analysis. Lambs in single births exceeded twins by 1.67 pounds, the difference being significant ($P < .01$). The type of birth was the second most important factor contributing to the variability of birth weight.

Two year-old ewes had offspring that were lightest at birth. Lambs from dams between four and seven years of age, were 0.48 and 1.16 pounds heavier than those from dams that were three and two years of age, respectively. Eight year-old ewes gave lambs that were heaviest at birth. Ram lambs weighed 0.46 pounds more than ewe lambs, the difference being highly significant.

The effect of breeding group was the most influential factor on the variation in birth weight. Lambs from the Navajo (N) breeding group were the smallest, being 1.61 and 1.80 pounds lighter than those from the coarse wool and fine wool groups, respectively.

The reduction in the total variability of birth weight by correcting for the effects of the environmental factors studied was 0.495 as measured by the multiple correlation coefficient (R^2); i.e. about 50 percent of the variance in birth weight in these data was due to the measured environmental differences that exist between individuals. Each of the factors involved had a highly significant effect on birth weight. Table 7 shows the percent of total variation attributed to each of these sources separately. Because the data were not orthogonal the percentage figures do not add to one hundred. The addition theorem for sums of squares is annulled due to unequality of subclass frequencies. The percentages indicate the relative importance of each different effect when uncorrelated with any other factor in the model.

Table 7. Percentage of total variance attributed to each main source of variation

Source of variation	Birth weight	Weaning weight (model I)	Weaning weight (model II)	Yearling body weight	Grease fleece weight	Clean fleece weight	Staple length	Fiber diameter
Years	4.03	26.76	22.18	16.72	11.49	18.86	6.62	32.04
Breeding group	18.46	2.72	0.04	1.31	21.37	7.36	13.23	22.39
Type of birth and rearing	16.61	17.01	7.08	1.14	3.88	2.48	0.27	0.11
Age of dam	7.58	4.92	1.67	0.45	1.20	1.19	0.27	0.27
Sex	1.58	3.52	2.07	27.89	8.77	11.87	3.73	2.15
Age of individual	--	5.08	6.75	0.26	1.42	0.84	0.25	0.34
Birth weight	--	--	5.14	--	--	--	--	--
Within main classes	50.53	33.91	39.14	20.09	42.00	43.59	73.57	43.30

2. Weaning weight

As mentioned in IV-A, two models were fitted for observations on weaning weight. The difference between the two models is that the regression of weaning weight on birth weight is not included in the first model and is in the second. For weaning weight, all the investigated factors had a highly significant effect (Tables 5, 6, and 7). Year of birth differences accounted for the major part of the variability. Type of birth and rearing rated second in influence on weaning weight, with single lambs weighing 6.06 and 13.89 pounds heavier than twins raised as singles and twin lambs, respectively.

Dams that were between four and seven years of age weaned the heaviest lambs, probably due to their greater potential in milk production. They exceeded lambs from two and three year old ewes and aged ewes by 7.25, 1.77 and 0.58 pounds. Ram lambs weighed 5.14 pounds more than ewe lambs, this difference being more important at weaning than at birth weight. The breeding group effect was lower in relative magnitude at weaning than it was at birth. Lambs of the N group weighed considerably less than lambs of both C and F groups, with a small difference between the latter two groups. It should be noted that breeding group effect which accounted for some 18.5 percent of total variation in birth weight, only accounted for 2.7 percent at weaning time. The regression of weaning weight on age of the lambs was 0.38 pounds per day. This of course does not represent the gain from birth to weaning. It represents the daily gain during a period of about 50 days encompassing the 120 day weight, since the lambs ranged from about 90 to 140 days of age at weaning time.

In the second model where birth weight was fitted as an independent continuous variable, the magnitude of the effect of some factors was changed, while others were not much affected. The most striking result was that the breeding group effect lacked significance in the second model. The significant effect observed in the first model was a result of initial difference in the birth weight of the three breeding groups. Tables 7, 8 and 9 show the least squares estimates and the analysis of variance of weaning weight when birth weight was considered in the model. Year differences show only a small change from the first model, while type of birth and rearing contribute much less to the total variability in weaning weight. Twin lambs raised as singles and as twins weighed 1.31 and 9.85 pounds less than lambs of single birth and rearing which is altered considerably. Still, dams ranging from four to seven years weaned the heaviest lambs, with the magnitude of differences being reduced. The difference between weaning weights of ram and ewe lambs, is smaller but is still in the same general direction, when influence of

Table 8. Mean, standard deviation, and least squares estimates of environmental factors on weaning weight (birth weight included)

Classification	Number of lambs	Estimate lb.	Standard error lb.
Mean	3264	55.170	
Standard deviation		7.504	
Years:			
1950	248	-10.04	.48
1951	78	-16.28	.80
1952	384	+ 9.70	.39
1953	260	- 0.10	.45
1954	324	- 0.30	.41
1955	244	- 4.07	.47
1956	291	+ 2.60	.43
1957	226	+ 6.62	.48
1958	249	- 2.24	.46
1959	291	- 0.72	.43
1960	340	+ 8.71	.42
1961	329	+ 6.12	.44
Type of birth and rearing:			
Single	2430	+ 3.75	.28
Twin	671	- 6.20	.29
Twin raised as single	163	+ 2.44	.42
Age of dam			
2 years	813	- 2.70	.36
3 years	725	+ 1.11	.34
4 - 7 years	1670	+ 1.72	.31
8 years or more	56	- 0.13	.78
Sex:			
Ram	1367	+ 2.00	.14
Ewe	1897	- 2.00	.14
Breeding group:			
N	886	- 0.49	.24
C	1454	+ 0.23	.20
F	924	+ 0.26	.21

Table 8. (Continued)

Classification	Number of lambs	Estimate lb.	Standard error lb.
Regression on age of lamb in days		+ 0.445	.018
Regression on birth weight of lamb		+ 2.450	.111
R^2		.661	

Table 9. Mean squares obtained from least squares analysis for weaning weight (birth weight included)

Source of variation	Degrees of freedom	Mean squares
Between years	11	10852.5**
Between breeding groups	2	116.8
Between types of birth and weaning	2	19064.3**
Between ages of dam	3	3001.1**
Between sexes	1	11123.1**
Between ages of lamb	1	36330.4**
Between birth weights	1	27646.3**
Residual	3242	56.3
Total	3263	

birth weight is removed. The regression of weaning weight on age was increased slightly to 0.445 pounds per day. Birth weight had a highly significant and important effect on weaning weight. This amounted to an increase of 2.45 pounds in weaning weight per one pound increase in the individual's birth weight above the average birth weight of all lambs studied.

3. Yearling body weight

Except for sex and year of birth, the remaining environmental factors showed less pronounced effect on yearling body weight than on the earlier weights, yet their individual contributions to the total variability in yearling weight were highly significant (Table 10). Single lambs weighed 7.16 and 2.32 pounds heavier than twins and twins raised singly, respectively (Table 11). Yearling lambs from two year-old and three year-old dams weighed 4.02 and 1.76 pounds less than those having dams between four and seven years of age, while the aged ewes had the heaviest lambs at yearling age. Since yearling body weight was obtained when the average age of individuals was about 400 days, the animals handicapped because of age of dam or type of birth effects had been able to overcome these disadvantages to a large extent. This is shown in Table 7 where their percentage contribution to total variability is much reduced from what

Table 10. Mean squares of yearling traits obtained from least squares analysis

Source of variation	Degrees of freedom	Yearling body weight	Grease fleece weight	Clean fleece weight	Staple length	Mean fiber diameter
Between years	10	12941**	45.5**	24.8**	58.9**	817.9**
Between breeding groups	2	5071**	423.5**	48.4**	588.4**	2858.4**
Between types of birth and rearing	2	4396**	76.9**	16.3**	12.2*	14.3
Between ages of dam	3	1171**	15.9**	5.2**	8.1	23.0*
Between sexes	1	215917**	347.5**	156.2**	331.6**	548.1**
Between ages of individual	1	1985**	56.5**	11.0**	22.0*	87.7**
Residual	1614	96.4	1.03	0.36	4.06	6.85
Total	1633					

Table 11. Means, standard deviations, and least squares estimates of environmental factors for yearling traits

Classification	No. of indi-viduals	Yearling weight (lbs.)		Grease fleece weight (lbs.)	
		Esti-mate	St. err.	Esti-mate	St. err.
Mean	1634	91.6		6.15	
Standard deviation		9.8		1.02	
Years:					
1950	221	-25.0	.9	-1.12	.07
1951	76	+ 3.3	1.1	+ .60	.11
1952	251	- 6.6	.6	- .11	.07
1953	161	- 3.0	.8	- .27	.08
1954	153	- 2.2	.8	- .26	.08
1955	91	- 5.1	1.0	- .26	.10
1956	160	- 1.8	.8	- .28	.08
1957	128	+ 5.5	.9	- .01	.09
1958	123	+ 7.9	.9	+ .11	.09
1959	119	+16.6	.9	+1.01	.09
1960	151	+10.4	.8	+ .60	.08
Type of birth and rearing					
Single	1329	+ 3.2	.5	+ .50	.05
Twin	221	- 4.0	.6	- .42	.06
Twin raised as singles	84	+ 0.8	.8	- .08	.08
Age of dam:					
2 years	278	- 2.8	.6	- .32	.07
3 years	373	- 0.6	.6	- .11	.06
4 - 7 years	943	+ 1.2	.5	+ .13	.05
8 years or more	40	+ 2.24	1.2	+ .31	.13
Sex:					
Ram	413	+14.03	.3	+ .56	.03
Ewe	1221	-14.03	.3	- .56	.03
Breeding group:					
N	397	- 4.03	.6	-1.09	.04
C	767	+ 1.57	.4	+ .18	.04
F	470	+ 2.66	.4	+ .92	.04
Regression on age in days		+ .169	.037	+ .026	.004
R^2		.80		.58	

Table 11. (Continued)

Classification	Clean fleece weight (lbs.)		Staple length (cms.)		Fiber diameter (microns)	
	Estimate	St. err.	Estimate	St. err.	Estimate	St. err.
Mean	3.39		10.04		25.61	
Standard deviation	0.60		2.01		2.62	
Years:						
1950	-1.05	.04	+ .51	.15	-4.35	.19
1951	+ .09	.07	-1.19	.22	+3.63	.29
1952	- .05	.04	- .34	.13	- .14	.17
1953	- .03	.05	- .76	.16	- .62	.21
1954	+ .07	.05	+1.15	.16	-1.85	.21
1955	+ .27	.06	+ .07	.20	-2.85	.26
1956	- .14	.05	- .39	.16	- .49	.21
1957	+ .14	.05	- .27	.17	+ .75	.23
1958	- .08	.05	+ .10	.18	- .17	.23
1959	+ .37	.05	+ .70	.18	+3.50	.23
1960	+ .42	.05	+ .42	.16	+2.54	.21
Type of birth and rearing						
Single	+ .25	.03	+ .24	.10	+ .21	.13
Twin	- .16	.04	- .05	.12	- .18	.18
Twin raised as singles	- .09	.05	- .18	.15	- .03	.20
Age of dam:						
2 years	- .18	.04	- .19	.13	- .38	.17
3 years	- .07	.04	- .03	.12	- .21	.16
4 - 7 years	+ .08	.03	+ .14	.11	+ .12	.14
8 years or more	+ .17	.08	+ .09	.25	+ .47	.33
Sex:						
Ram	+ .38	.02	+ .55	.06	+ .71	.08
Ewe	- .38	.02	- .55	.06	- .71	.08
Breeding group:						
N	- .36	.02	+ .18	.08	+1.44	.11
C	+ .31	.02	+ .98	.07	+1.40	.10
F	+ .05	.02	-1.15	.08	-2.84	.10
Regression on age in days	+ .012	.002	+ .017	.007	+ .033	.009
R^2	.56		.26		.57	

it was at weaning and birth weights. Sex was the most influential single factor on yearling weight, with rams exceeding ewes by 28.06 pounds. Also year of birth differences contributed importantly to the variability in yearling weights, which may be attributed to general climatic and grazing conditions which prevail in different years. However, genetic trend or progress is also confounded with year effects. Selection may be a reason for the large sex difference because the number of rams retained is much less than the number of ewes. The Navajo breeding group still showed lower body weight than both the Finewool and Coarsewool groups, the Finewool group being slightly heavier. The linear regression of yearling body weight on yearling age was 0.168 pounds per day.

When weaning weight was added to the model as an independent continuous variable, the effects of type of birth and rearing and age of dam lacked significance, and the effect of type of birth changed sign. The least squares estimates of types of birth showed that singles were 1.00 and 0.41 pounds lighter than twins and twins raised as singles. Tables 12 and 13 show that the magnitude of effects in the different subclasses was reduced, but only a little in the case of year of birth and sex effects. The regression on yearling age changed in sign to a value of -0.102, pounds per day which was significantly different from zero. Yearling body weight

Table 12. Means, standard deviations, and least squares estimates of environmental factors for yearling traits (weaning weight included)

Classification	No. of individuals	Yearling body weight (lbs.)	Grease fleece weight (lbs.)	Clean fleece weight (lbs.)	Staple length (cms.)	Fiber diameter (microns)
Mean	1634	94.13	5.59	3.16	9.60	24.76
Standard deviation		8.52	0.98	0.58	2.01	2.62
Years:						
1950	221	-20.00	-0.66	-0.81	+0.53	-4.21
1951	76	+15.65	+1.36	+0.48	-1.16	+3.86
1952	251	-14.15	-0.58	-0.28	-0.37	-0.28
1953	161	- 2.47	-0.32	-0.06	-0.76	-0.64
1954	153	- 1.61	-0.27	+0.06	+1.15	-1.85
1955	91	- 5.43	-0.07	+0.36	+0.08	-2.79
1956	160	- 3.66	-0.39	-0.20	-0.40	-0.52
1957	128	+ 1.82	-0.31	-0.01	-0.28	+0.66
1958	123	+10.77	+0.21	-0.03	+0.11	-0.14
1959	119	+16.88	+0.98	+0.35	+0.70	+3.53
1960	151	+ 2.18	+0.06	+0.15	+0.40	+2.39
Type of birth and rearing						
Single	1329	- 0.47	+0.29	+0.14	+0.23	+0.15
Twin	221	+ 0.53	-0.16	-0.03	-0.04	-0.11
Twin raised as single	84	- 0.06	-0.13	-0.11	-0.19	-0.05

Table 12. (Continued)

Classification	No. of individuals	Yearling body weight (lbs.)	Grease fleece weight (lbs.)	Clean fleece weight (lbs.)	Staple length (cms.)	Fiber diameter (microns)
Age of dam:						
2 years	278	- 0.52	-0.19	-0.11	-0.19	-0.34
3 years	373	- 0.89	-0.13	-0.08	-0.03	-0.22
4 - 7 years	943	- 0.39	+0.03	+0.03	+0.14	+0.09
8 years or more	40	+ 1.80	+0.29	+0.16	+0.09	+0.47
Sex:						
Ram	413	+10.75	+0.38	+0.28	+0.54	+0.65
Ewe	1221	-10.75	-0.38	-0.28	-0.54	-0.65
Breeding group:						
N	397	- 1.28	-0.94	-0.28	+0.18	+1.48
C	767	+ 0.01	+0.09	+0.26	+0.97	+1.38
F	470	+ 1.26	+0.85	+0.01	-1.18	-2.86
Regression on age in days		- 0.102	+0.012	+0.005	+0.016	+0.029
Regression on weaning weight		+ 0.779	+0.045	+0.022	+0.002	+0.013
R^2		0.85	0.61	0.59	0.26	0.57

Table 13. Mean squares of yearling traits obtained from least squares analysis (weaning weight included)

Source of variation	Degrees of freedom	Yearling body weight	Grease fleece weight	Clean fleece weight	Staple length	Fiber diameter
Between years	10	14124**	41.4**	17.6**	58.9**	738.6**
Between breeding groups	2	627**	306.0**	29.9**	588.5**	2843.1**
Between type of birth and rearing	2	66**	17.0**	3.6**	9.5	5.1
Between ages of dam	3	85	5.4**	2.1**	7.1	17.9*
Between sexes	1	96968**	118.2**	67.2**	318.9**	356.5**
Between ages of individual	1	634**	10.9**	1.5*	18.0*	59.5**
Between weaning weights	1	38397**	125.6**	31.8**	0.3	10.9
Residual	1613	72.6	0.95	0.34	4.06	6.85
Total	1633					

increased 0.78 pounds for each pound of increase in weaning weight.

The estimates obtained from analyzing the ewe data alone did not differ much from those obtained in the first analysis where both sexes were represented. Differences due to age of dam were not as large as in the combined analysis, and the regression on age was about 0.03 pounds less. Year differences accounted for more of the variability than in the analysis of both sexes.

4. <u>Grease fleece weight</u>

Yearly differences were an important source of variation, accounting for some 11.5 percent of total variation in grease fleece weight (Table 7). The effect of breeding group was the major source of variability, being responsible for 21.4 percent of the variation. The Finewool group produced 2.01 and 0.74 pounds of wool more than the Navajo and Coarsewool groups, while the difference between the latter two groups was 1.27 pounds in favor of the C group. Yearling rams exceeded ewes by 1.13 pounds of wool. Single born lambs sheared 0.91 and 0.58 pounds more than twins and twins raised singly, respectively. Offspring from aged ewes produced more wool than offspring from dams of other ages. They sheared 0.64, 0.43 and 0.19 pounds more than individuals that had dams of two, three and four to seven years of age, respectively. The regression of fleece weight on age at shearing was 0.026 pounds per day.

No change occurred in the signs of the effects of the factors when weaning weight was included in the model, but their magnitudes were reduced, while their effects were still significant. The regression on age at shearing was much reduced from a value of 0.026 to 0.012 pounds per day.

Year of birth and differences among breeding groups accounted for more of the variability of grease fleece weight in the ewe data.

5. Clean fleece weight

Clean fleece weight was affected significantly by the environmental differences studied. Year and sex contributed more to variability of clean fleece weight than of grease weight, while breeding groups showed a considerably lower effect (Table 7). Rams exceeded ewes by 0.75 pounds, and single born lambs gave 0.40 and 0.33 pounds more of clean fleeces than twins and twins raised as singles, respectively. The C breeding group, as expected, gave higher weights of clean wool than the F and N groups, with the latter producing the smallest quantity.

In the analysis of clean fleece weight, year effects were more pronounced than in the combined data only in the yearling ewes

6. Staple length

The influence of environmental factors on staple length was considerably smaller than their effects on the other traits studied. Year of birth, breeding group and sex differences were highly significant, accounting for 6.6, 13.2 and 3.7, percent, respectively, of the total variation. Type of birth and rearing accounted for a small part of the variability, but was significant, while the influence of age of dam was not significant for this trait. The most important source of variation was differences among breeding groups. Yearlings of the coarse-wool group had the longest staple, exceeding those from the Navajo and the finewool groups by 0.80 and 2.13 centimeters, respectively. The statistically significant regression of staple length on age was 0.017 centimeters per day.

When the regression of staple length on weaning weight was included in the model, both the type of birth and rearing and age of dam showed no significant effect on staple length. Also, the regression on weaning weight was not significant (Table 13). This may be due to age of dam and type of birth exerting most of their effects on staple length through their influences on weaning weight. The least squares estimates of each of the effects obtained from the ewe data were significant (Tables 14 and 15).

Table 14. Means, standard deviations and least squares estimates of environmental factors for yearling traits in ewes

Classification	No. of individuals	Yearling body weight (lbs.)	Grease fleece weight (lbs.)	Clean fleece weight (lbs.)	Staple length (cms.)	Fiber diameter (microns)
Mean	1190	77.85	4.89	2.72	9.03	24.08
Standard deviation		8.25	0.92	0.53	1.53	2.34
Year:						
1950	207	-26.11	-1.12	-1.04	+0.58	-4.32
1951	50	+ 3.06	+0.64	+0.09	-1.30	+3.80
1952	206	- 7.76	-0.26	-0.12	-0.36	-0.77
1953	114	- 2.31	-0.24	-0.08	-0.88	+0.00
1954	101	- 5.54	-0.47	-0.09	+1.48	-3.08
1955	52	- 3.93	-0.42	+0.11	-0.10	-2.77
1956	105	+ 6.45	+0.33	+0.22	-0.01	+0.72
1957	78	+ 4.85	+0.16	+0.31	-0.45	+1.20
1958	86	+ 9.39	+0.22	-0.04	+0.13	-0.57
1959	80	+12.77	+0.92	+0.42	+0.47	+3.10
1960	111	+ 9.12	+0.24	+0.22	+0.43	+2.68
Type of birth and rearing:						
Single	938	+ 2.59	+0.45	+0.22	+0.28	+0.09
Twin	185	- 4.11	-0.39	-0.16	-0.26	-0.10
Twin raised as single	67	+ 1.51	-0.06	-0.06	-0.03	+0.01

Table 14. (Continued)

Classification	No. of individuals	Yearling body weight (lbs.)	Grease fleece weight (lbs.)	Clean fleece weight (lbs.)	Staple length (cms.)	Fiber diameter (microns)
Age of dam:						
2 years	212	- 1.95	-0.27	-0.15	-0.23	-0.26
3 years	262	+ 0.35	-0.02	-0.02	+0.04	-0.10
4 - 7 years	681	+ 0.74	+0.13	+0.08	+0.13	+0.21
8 years or more	35	+ 0.96	+0.16	+0.08	+0.06	+0.15
Breeding groups:						
N	302	- 3.77	-0.99	-0.27	+0.31	+1.65
C	560	+ 1.53	+0.16	+0.28	+0.78	+1.23
F	328	+ 2.25	+0.84	-0.01	-1.09	-2.89
Regression on age in days		+ 0.129	+0.022	+0.010	+0.018	+0.018
R^2		0.72	0.53	0.47	0.33	0.61

Table 15. Mean squares of yearling traits obtained from least squares analysis for ewes

Source of variation	Degrees of freedom	Yearling body weight	Grease fleece weight	Clean fleece weight	Staple length	Fiber diameter
Between years	10	9621**	32.8**	19.99**	52.66**	664.3**
Between breeding groups	2	3237**	256.4**	25.74**	319.62**	2033.8**
Between types of birth and rearing	2	3091**	52.1**	10.62**	21.04**	2.3
Between ages of dam	3	366**	8.2**	2.65**	6.50*	13.3
Between ages of individual	1	854**	30.2**	5.87**	19.53**	19.8
Residual	1171	68.1	0.84	0.279	2.339	5.45
Total	1189					

7. <u>Fiber diameter</u>

Differences among years, breeding groups, and sexes were highly significant for fiber diameter. As shown in Table 7, year and breeding group accounted for practically all of the contribution of the known environmental factors to the variation in fiber diameter. It must be stressed again that a large part of the yearly trend may be genetic, resulting from selection. Type of birth and rearing did not show any significant effect on fiber diameter. The regression on weaning weight also was not significant when it was fitted in the second model (Table 13).

From the analysis conducted on the yearling ewes only, year of birth and breeding group differences influenced the variation in fiber diameter significantly (Table 15).

B. Estimates of Heritability

The method of calculating heritability by computing paternal half-sib correlations from the pooled sums of squares between sires and within sires was mentioned in IV B-1. The analysis of variance was performed on the adjusted records for the seven traits studied, as shown in Table 16. The heritability estimates were thus calculated on an intra sire, year, and breeding group basis, and are presented in Table 17.

In the present data the number of comparisons between

Table 16. Analysis of variance of adjusted records for all characters studied

Source of variation	Degrees of freedom	Sum of squares	Mean squares	Expected mean squares	Variance component
Birth weight					
Between breeding group-year	35	2582.03	73.772	$\sigma_e^2+k_2\sigma_s^2+k_3K_{BG}^2$	0.790
Between sires BG-YR	167	423.46	2.536	$\sigma_e^2+k_1\sigma_s^2$	0.079
Within sires	3049	4131.85	1.355	σ_e^2	1.355
	3251				
		$k_1 = 15.01$			
Weaning weight					
Between breeding group-year	35	163309.0	4666.0	$\sigma_e^2+k_2\sigma_s^2+k_3K_{BG}^2$	50.790
Between sires BG-YR	167	17029	102.0	$\sigma_e^2+k_1\sigma_s^2$	3.048
Within sires	3045	171341	56.27	σ_e^2	56.270
	3247				
		$k_1 = 15.00$			

Table 16. (Continued)

Source of variation	Degrees of freedom	Sum of squares	Mean squares	Expected mean squares	Variance component
<u>Yearling weight</u>					
Between breeding group-year	35	253387.0	7239.63	$\sigma_e^2+k_2\sigma_s^2+k_3K_{BG}^2$	141.537
Between sires BG-YR	165	19842.0	120.25	$\sigma_e^2+k_1\sigma_s^2$	4.210
Within sires	1628	136430.0	83.80	σ_e^2	83.802
	1828				
		$k_1 = 8.66$			
<u>Grease fleece weight</u>					
Between breeding group-year	35	1629.0	46.54	$\sigma_e^2+k_2\sigma_s^2+k_3K_{BG}^2$	0.875
Between sires BG-YR	165	319.6	1.94	$\sigma_e^2+k_1\sigma_s^2$	0.114
Within sires	1642	1542.8	0.94	σ_e^2	.940
	1842				
		$k_1 = 8.72$			

Table 16. (Continued)

Source of variation	Degrees of freedom	Sum of squares	Mean squares	Expected mean squares	Variance component
Clean fleece weight					
Between breeding group-year	35	417.7	11.94	$\sigma_e^2+k_2\sigma_s^2+k_3K_{BG}^2$	0.223
Between sires BG-YR	165	109.2	0.66	$\sigma_e^2+k_1\sigma_s^2$	0.038
Within sires	1623	549.4	0.34	σ_e^2	0.338
	1823	$k_1 = 8.62$			
Staple length					
Between breeding group-year	32	2148.5	67.14	$\sigma_e^2+k_2\sigma_s^2+k_3K^2$	1.209
Between sires BG-YR	156	852.3	5.46	$\sigma_e^2+k_1\sigma_s^2$	0.201
Within sires	1504	5639.5	3.75	σ^2	3.750
	1692	$k_1 = 8.54$			

Table 16. (Continued)

Source of variation	Degrees of freedom	Sum of squares	Mean squares	Expected mean squares	Variance component
Fiber diameter					
Between breeding group-year	32	14095.0	440.47	$\sigma_e^2+k_2\sigma_s^2+k_3K_{BG}^2$	8.494
Between sires BG-YR	156	1441.7	9.24	$\sigma_e^2+k_1\sigma_s^2$	0.331
Within sires	1506	9644.8	6.40	σ_e^2	6.404
	1694				

$k_1 = 8.56$

Table 17. Intraclass correlations and heritability estimates obtained from analysis of variance of traits studied

Trait	Heritability	Standard error
Birth weight	.220	±.050 ±.032[a]
Weaning weight	.206	±.049
Yearling weight	.192	±.072
Grease fleece weight	.436	±.088
Clean fleece weight	.400	±.088
Staple length	.204	±.076
Fiber diameter	.196	*.072

[a]Estimated from formula in IV-B-1 where n_o is variable.

sets of twins was 1.5 percent of the total number of comparisons among offspring of the same sire. Accordingly it was thought not important to adjust the intraclass correlations for that effect. Hazel and Terrill (1945b) reported that it was not necessary to correct heritability estimates they obtained for the comparisons that are between full sibs in the analysis of half-sib correlations, since only about 1.3 percent of their comparisons were between sets of twins within sire groups.

The heritability estimate of .22 obtained for birth weight was in agreement with most of those reported in the literature. It was far smaller than the .72 reported by Nelson and Venkatachalam (1949) using the same method, but did not differ much from their estimate from the regression method. On the other hand, it exceeded the estimates given by Cassard and Wier (1956), and by Butcher and Welch (1964) using both paternal half sibs and intra-sire regression of offspring on dam (Table 1).

Estimates of heritability of weaning weight which are in a substantial agreement with the 0.21 value obtained here are reported by Hazel and Terrill (1946) as an average of two methods, Sidwell (1954) analyzing Navajo crossbred dam-offspring pairs, Shelton (1959), Shelton and Campbell (1962) using the regression method, and Botkin (1964) using the correlation between paternal half-sibs. The estimates found here are considerably higher than those reported by Ali (1952), Ragab _et al_. (1953), Kyle and Terrill (1953) using both ewes and rams separately, Blackwell and Henderson (1955), Givens _et al_. (1960), and Carter and McClure (1962) using both regression of offspring mean on sire record and half-sib correlations. Substantially higher estimates have been found by Hazel and Terrill (1945) using the same method used here and regression of offspring on dam, Nelson and Venkatachalam (1949), Ali (1952) obtained from the regression method, Karam et al. (1953), Cassard and Weir (1956), Warwick and Cartwright (1957) using three regression estimates of offspring on mid-parent, sire performance, and on dam. Also, higher estimates have been reported by MacNaughton (1956), Dalton (1962), Shelton and Campbell (1962), and Botkin (1964) who used the correlation among full-sibs.

The heritability of yearling body weight found in this study was .19. This is generally lower than the estimates reported by other investigators. The only two lower estimates found were given by Morley (1955) and Balch (1962) both using paternal half-sib correlations. However, the values found in this study are in good agreement with those showed by Morley (1951) and Kyle and Terrill (1953) who used the same method employed in this work. All other values that were found in the literature are considerably higher, such as those given by Terrill and Hazel (1943), Morley (1951, 1955), MacNaughton (1956), Young et al. (1960) and Hall et al. (1964).

An estimate of .44 for the heritability of grease fleece weight was found in this investigation, which agrees well with the majority of estimates that have been reported, including Rasmussen (1942), Cockerham (1949), and Morley (1951, 1955) using the regression of offspring on dam and paternal half-sib correlations. Also it coincides closely with those values given by Blackwell and Henderson (1953), Felts et al. (1957), and Young et al. (1960). Considerably lower estimates were obtained by McMahon (1943), Rae (1948, 1950), and Kyle and Terrill (1953). On the other hand, substantially higher estimates were found by Morley (1951) using paternal half-sib correlations, Kyle and Terrill (1953) working with data from ewes only, Ali (1952), Wright and Stevens (1953), Dalton (1962), and Balch (1962).

The heritability of clean fleece weight estimated from the data used here does not differ considerably from those reported by Terrill and Hazel (1943), Morley (1955), and Young et al. (1960). Morley (1951), and Kyle and Terrill (1953) obtained higher estimates, while lower values were shown by Kyle and Terrill (1953) using data from ewes only, and Hall et al. (1964).

The heritability estimates obtained here for both staple length and fiber diameter fall in the low range and are considerably lower than those reported in the literature for these traits. Morley (1951), Rae (1948), Kyle and Terrill (1953) and Hall et al. (1964) obtained values for the heritability of staple length that are in general agreement with those found here. Intense selection for both of these traits could have slightly reduced the additive genetic variance among sires.

Heritability was also determined by computing the regression of the offspring's record on dam's record, as mentioned previously in IV-B-2. To remove the variation due to measurable environmental effects, the records of the offspring were adjusted for type of birth and rearing, sex, and age of individual, using the correction factors obtained in V-A. Corrections employed to adjust the dam records were those due to differences in type of birth and rearing and due to the regression on age, which were obtained from the least squares analysis of the ewe data only in V-A. The effect of age of dam was eliminated by doing the analysis within years of birth of dams. Hence the comparisons between offspring and dam were freed from bias due to age of dam and also due to the dams being born in years when the average was higher or lower. The results within year of dam were combined by pooling the sums of squares, sums of crossproducts and degrees of freedom, and the regressions were computed from the pooled results.

Doubling the regression of offspring on dam, calculated within year of dam, sire, year of offspring, and breeding group, gives the heritability estimates shown in Table 18 in the diagonal under sub-heading 2.

All the heritability estimates obtained from the regression method were higher than those obtained from the half-sib correlation method, except for clean fleece weight. This could be partly due to selection of sires having reduced the sire component in the correlation method, while the

Table 18. Genetic correlations and heritabilities

Traits	Method of analysis	Birth weight	Weaning weight	Yearling weight	Grease fleece weight	Clean fleece weight	Staple length	Fiber diameter
Birth weight	Method 1[a]	--	--	.145	0	0	-.185	-.254
	Method 2[b]	--	--	.137	-.068	-.129	-.166	-.231
	Method 3[c]	.366[d]	.125[d]	0	0	.143	-.018	0
	Method 4[e]	--	.425[d]	.363	-.091	.187	-.097	-.311
Weaning weight	Method 1		--	1.153	0	0	-.242	0
	Method 2		--	1.209	.238	-.450	-.313	-.190
	Method 3		.294[d]	1.322	0	0	-.431	0
	Method 4		--	1.325	.048	-.104	-.480	-.088
Yearling weight	Method 1			.245	0	-.875	-.537	-.098
	Method 2			--	-.232	-.883	-.146	-.176
	Method 3			.531	.036	0	-.591	.065
	Method 4			--	.036	-.170	-.677	-.224

[a]Method 1 - analysis within sires, geometric means used (605 d.f.).

[b]Method 2 - analysis within sires, arithetic means used (605 d.f.).

[c]Method 3 - analysis within year of dam, geometric means used (148 d.f.).

[d]1376 d.f. available.

[e]Method 4 - analysis within year of dam, arithmetic means used (148 d.f.).

Table 18. (Continued)

Traits	Method of analysis	Birth weight	Weaning weight	Yearling weight	Grease fleece weight	Clean fleece weight	Staple length	Fiber diameter
Grease fleece weight	Method 1				.285	.782	0	0
	Method 2				--	.793	.196	.035
	Method 3				.487	.877	0	0
	Method 4				--	.869	.075	.021
Clean fleece weight	Method 1					.127	0	.057
	Method 2					--	.470	.191
	Method 3					.312	0	.077
	Method 4					--	.118	.196
Staple length	Method 1						.291	.117
	Method 2						--	.175
	Method 3						.325	0
	Method 4						--	.027
Fiber diameter	Method 1							.269
	Method 2							--
	Method 3							.406
	Method 4							--

regression is free of this effect, and may be also due to elimination of the variability due to the year of dam effect. However, there was no tendency to assortively mate some sires to dams born in particular years. This will randomize the year of dam effect between the between and within sire components of variance and consequently will render unbiased estimates of the variance components.

These estimates agree more closely with those reported in the literature, with those of birth weight and yearling body weight being in the higher range of estimates reported.

The estimates for yearling body and wool traits were determined from those records that had all values of the five traits appearing, while those for birth and weaning weight were calculated from all records that showed both of these traits. Accordingly considerably more degrees of freedom were available for the latter than for the yearling traits.

C. Genetic Correlations

The genetic correlations among body weights at different ages, among fleece traits, and between body weights and fleece characters are shown in Table 18. As mentioned before in IV-C, these correlations were computed from the same analysis as was used in calculating the heritabilities by the regression method. The covariances between the traits on the dams and their offspring, needed for calculating the genetic correlations according to the formula given in II-D, are presented in Table 19. The genetic correlations could also be obtained by using the arithmetic average of the covariances, rather than the geometric mean, according to the following formula.

$$r_{G_x\,G_y} = \frac{\text{Cov } X_D\, Y_0 + \text{Cov } Y_D\, X_0}{2\sqrt{\text{Cov } X_D\, X_0 \cdot \text{Cov } Y_D\, Y_0}}$$

where X and Y are the two correlated traits while (D) subscript refers to the trait on the dam, and (O) refers to the trait on the offspring.

The results obtained by using both formulae were shown in Table 18. Two analyses were performed. The first one was within year of birth of dam, sire, year of birth of individual, and breeding group, and the correlations were estimated from the mean squares and mean cross-products within year of dam. In the second analysis the within year of dam and between year of dam sums of squares and cross-products were pooled, and the correlations hence were obtained. The genetic correlations between birth weight and weaning weight were estimated only from the first analysis because a large number of individuals showed both these traits. The genetic correlations between weaning and yearling traits were estimated only from individuals that had all seven characters.

Table 19. Mean covariances between traits studied

Trait on dams	Method of analysis	Trait on offspring: Birth weight	Weaning weight	Yearling weight	Grease fleece weight	Clean fleece weight	Staple length	Fiber diameter
Birth weight	Method 1[a]	--	--	.448	.037	.032	-.040	-.215
	Method 2[b]	.220	.275	-.126	.026	.033	.0	-.357
Weaning weight	Method 1	--	--	12.356	.568	.115	-.161	.061
	Method 2	.728	5.783	11.842	.317	.072	-.380	-.685
Yearling weight	Method 1	.152	6.632	11.629	-.599	-.371	-.855	-.105
	Method 2	1.507	13.361	13.607	.067	.072	-.702	-.717
Grease fleece weight	Method 1	-.065	-.183	.048	.121	.045	.111	.015
	Method 2	-.030	-.213	.046	.180	.076	.112	-.013
Clean fleece weight	Method 1	-.055	-.408	-.481	.033	.020	.098	.018
	Method 2	.007	-.183	-.332	.077	.043	.082	.007
Staple length	Method 1	-.088	-.717	-1.462	-.028	-.017	.372	.028
	Method 2	-.074	-.980	-2.044	-.077	-.055	.302	-.009
Fiber diameter	Method 1	-.089	-.968	-1.135	-.040	.038	.193	1.072
	Method 2	.065	.127	-.792	.029	.067	.036	.830

[a]Method 1 - analysis within sires, year-breeding group.

[b]Method 2 - analysis within year of dam, sire, year-breeding group.

Thus, all covariances between different weaning and yearling traits were based on the same number of degrees of freedom.

One of the correlations, namely that between weaning and yearling weights, is larger than unity. This discrepancy must be due to sampling errors which are large for genetic correlations, or to having some real non-genetic covariance in the numerator.

Negative genetic correlations were found between body weights at the different stages of life and the wool traits, except for the positive ones found between grease fleece weight and weaning weight, and that between grease fleece weight and yearling body weight for the second method. These agree with the results reported by Hall _et_ _al_. (1964) using material from the same flock. No estimates were found in the literature for the genetic correlations between birth weight and yearling fleece traits. Ragab _et_ _al_. (1953) reported an estimate of 1.04 for the genetic correlation between birth weight and weaning weight on Ossimi sheep. However, MacNaughton (1956) obtained .24 and .54 as an estimate for that correlation in Rambouillets and Corriedales, respectively. The value calculated in this study for that correlation is in agreement with that found by MacNaughton in his Corriedale sheep, while it is far less than that of Ragab _et_ _al_. (1953). The correlation between birth weight and yearling body weight obtained from the second method is .36, which is in substantial agreement with those found by MacNaughton for both breeds, while the estimate obtained by Ragab _et al_. far exceeds the one found in this study. However, Ragab _et al_. reported a value of .96 for the correlation between weaning weight and market weight (8 months) which, like the one found here, is very high. Lower estimates for the genetic correlation between those two traits have been reported by MacNaughton (1956) and Balch (1962).

The genetic correlations between the fleece characters are in general agreement with those reported in the literature (Table 3). Higher estimates were obtained by Rae (1950) and Balch (1962), while lower values were given by Morley (1950) and by Hall _et al_. (1964).

D. Phenotypic Correlations

Table 20 shows the observed phenotypic correlations between the seven weanling and yearling traits. As mentioned previously in IV-D, the phenotypic correlations were calculated from the pooled analysis of variance within year of birth of dam, sire, year of birth of lamb, and breeding-group. The correlations found between body weights at different ages, and fleece traits, namely, staple length and mean fiber diameter, were very small, except for that between yearling body weight and fiber diameter. This latter correlation is somewhat higher than those reported in the

Table 20. Phenotypic correlations

Trait	Weaning weight	Yearling weight	Grease fleece weight	Clean fleece weight	Staple length	Fiber diameter
Birth weight	.361	.284	.221	.243	.016	.002
Weaning weight		.479	.236	.199	.028	.017
Yearling weight			.430	.477	-.030	.266
Grease fleece weight				.799	.128	.291
Clean fleece weight					.284	.286
Staple length						-.071

literature (Table 2), but is in general agreement with those found by Morley (1950) and Terrill and Kyle (1953). In general the correlations found between body weights are slightly lower than those reported in literature, but are in the same directions. The phenotypic relationships found between fleece traits agree closely with those reported by other workers, except that lower values were found here for the correlations involving staple length. A small negative correlation was found between staple length and fiber diameter, which agrees with that shown by Jones *et al*. (1944), but is not consistent with the other estimates reported.

VI. DISCUSSION

How far can one proceed in generalizing estimates obtained from this sample to other populations is debatable. Estimates of environmental, phenotypic and genetic parameters need not be constants applicable to all other populations. Rather they are estimates of the parameters which pertain to a given flock at a given period. On the other hand, if the direction, and possibly the magnitude, of estimates obtained from differing flocks at different times are rather consistent, this gives some confidence that they have some general biological causes and will be nearly the same in still other flocks and at other times.

Environmental differences can influence the expression of traits, and this in turn will be reflected in the resulting estimates. However, if one could not apply the available information to other situations at all, investigation would be useless since no two actual cases ever are exact duplicates. Applicability is limited by possibility of real differences among populations, as well as by the internal sampling errors of the data in the sample studied. Examining the results obtained in this study may provide useful evidence of the important factors operating in this flock and may indicate - although with less confidence - those expected to be important in other flocks.

A. Phenotypic Statistics

Environmental and fixed factors such as year of birth, type of birth, age of dam, sex, and age of lamb are very important sources of variation. Evaluating their effects gives the ability to correct the data accordingly. This can prevent some of the errors the breeder would otherwise make in selecting individuals for replacement and for improving his production.

Year of birth of lamb had an important effect on all traits studied. Presumably the year effects are due primarily to the amount of precipitation that falls within a year. This could affect a trait either directly or indirectly. For example the effect of years on birth weight of the lamb is exerted primarily through the amount of feed his mother is able to get. This is a common situation with sheep that are raised under arid conditions where only small quantities of supplemental feed, or none at all, is given. Other than the amount of rain, management practices and variations in the general health of the flock could act also as a part of the year effects. Also confounded with the year differences can be any genetic trend which existed. The amount of dirt and plant material in the grease fleece could vary from year to year depending on the prevailing weather conditions.

Terrill *et al.* (1947), investigating the effects of different environmental factors on Columbia and Targhee sheep, found yearly differences to be the most important source of variation on body weight and fleece traits at yearling age. Sidwell (1948), working with Navajo sheep, from the same source as those at hand, found that differences among year of birth had major and significant effects on weaning weight. In the present study, differences from year to year were very important sources of variation, with year means reaching differences as much as 28.3 pounds at weaning time. Due to drouth for six consecutive years the numbers were reduced from 384 in 1952 to 226 in 1957. This period was especially difficult for ewes carrying lambs and for aged ewes, many of which were not strong enough to survive. Culling in some years was done earlier than usual in order to conserve forage, a practice which will not give lambs a chance to attain their genetically determined weights. Many local ranchers even cut pinon trees to provide forage for their sheep.

The effect of type of birth was the second most important influence on birth and weaning weights, but showed less pronounced effects on yearling body weight and fleece traits. This was anticipated since the handicap imposed on the twin-born-lambs might be overcome by the time both singles and twins reach yearling age. Intra-uterine competition between twins is severe for the nourishment supplied by the mother. This causes the twins to weigh less than single born lambs, a difference of 1.67 pounds in this study. After birth the competition between the twins for milk is the major cause for the difference in weight observed between twin and single-born lambs. A part of this difference is overcome if one of the twin-born lambs is fostered on another mother. The difference between weaning weight of single born lambs and those born as twins but raised singly was 6.06 pounds, while the singles were 13.89 pounds heavier than twins raised as twins. Chapman (1931) found type of birth had the most pronounced effect on birth weight. This has been a widely accepted fact supported by the findings of Nelson and Venkatachalam (1949), Yao et al. (1953), Blackwell and Henderson (1955) and MacNaughton (1956), Bogart et al. (1957) and Sidwell et al. (1964). This effect of type of birth seems to be even magnified by the time animals reach weaning age, with those twins reared as singles not attaining the same weight as singles due to the earlier handicap at birth, but considerably exceeding those reared as twins. Hazel and Terrill (1945a, 1946a) substantiate the results found here for the type of birth and rearing effects on weaning weight. Sidwell and Grandstaff (1949) working with Navajo sheep found that singles exceeded twins and twins raised singly by 11.2 and 2.9 pounds, respectively. When birth weight was kept constant by including it in the model as a concomitant variable, the type of birth had less effect on weaning weight.

Single born lambs weighed 1.31 and 9.95 pounds more than twins raised as twins and those twins raised as twins, respectively. De Baca et al. (1956) obtained results that agreed with those found in this work. They observed that the advantage which singles had over twins was reduced from 17 pounds to 8.8 pounds when regression of weaning weight on birth weight was included in the model of analysis.

By the time individuals reach yearling age type of birth has less effect on either body weight or fleece traits, due to the ability of twins partly to overcome the earlier handicap (Table 11). In this respect the differences in yearling body weight found in this study were 7.2 and 2.3 pounds for singles over twins and over twins raised as singles, respectively. This decline in the effect of type of birth has been shown by many workers including Phillips and Dawson (1940), Simmons (1943), Hazel and Terrill (1946c), Balch (1962), and Hall et al. (1964), who worked with data on ewes from the same source as the one at hand. The same general trend was also observed with regard to the wool traits. However, Terrill et al. (1947) found some results in Targhee ewes that did not agree with their findings in Columbia sheep. Singles exceeded twins by 4.7 pounds and exceeded twins raised as singles by 7.4 pounds at yearling. It could be that in the Targhee breed many of the twins were culled earlier in life because they did not attain the desired weights, and those highly selected twins that were present as yearlings do not represent the whole population of twin lambs.

In this work it was observed that when weaning weight was included as an independent variable in the model for yearling body weight, single born lambs were 1.0 and .41 pounds lighter as yearlings than twins and twins raised as singles, respectively. This may mean that when weaning weight is kept constant, the post-weaning gains of twin lambs exceed those of single born lambs.

The age of the dam exerts most of its influence on the pre-weaning traits and less on post-weaning ones. In this study, age of dam had its most pronounced effects on both birth and weaning weights compared with yearling body and wool traits.

Eight year-old and older ewes gave birth to lambs heavier than those from four to seven, three, and two year old ewes in that order. On the other hand, lambs weaned from four to seven year-old dams attained the highest weaning weight, followed by lambs from eight or more, three, and two year old ewes, respectively. This could be due to older ewes providing a better intra-uterine environment than younger ewes, but not being as efficient milk producers. Accordingly one might expect lambs from aged ewes to have a higher weight at birth, but somewhat lighter weaning weight than those from mature ewes. Many workers have shown that milk production is higher in mature ewes than two year-old ewes. Barnicoat _et al._ (1949) have shown that six year-old ewes produced 15 percent more milk than two year-old ewes. Bonsma (1939) found that the supply of milk increased by 25 percent from the first to the third lactation. Yalcin and Bichard (1964) showed that the birth weight of the lambs from seven year-old dams were higher than those from five and six years-old, but about equal to lambs born to four year-old ewes. Also Montanaro (1940) showed that in Sicilian dairy sheep, milk production reached a maximum in the fifth lactation and subsequently declined. Rae (1946) observed that the birth weights of lambs from five year-old ewes were higher than those from two year-old ewes. Examining the results from the model in which birth weight was included as an independent variable helps to understand these relations. When birth weight was kept constant the weaning weights of lambs from ewes of the four to seven age bracket exceeded those from two, three and eight or more years of age by 4.4, 0.6, and 1.8 pounds, respectively. This suggests an advantage for milk production of the four to seven and three year-old groups over ewes that are either two years of age or eight or more years old, since their lambs achieved higher weaning weights at a constant birth weight. Blackwell and Henderson

(1955) found a significant linear regression of birth weight of lamb on age of the dam amounting to .71 pounds per year, and a significant, but small positive quadratic term of .06 pounds. Meanwhile, the results they found at weaning time were 3.1 and -.31 pounds for the linear and quadratic terms, respectively, reaching a maximum at five years of age, which supports the results obtained here. Kincaid (1943) stated that birth weight of lambs increased .63 pounds per year as the ewes increased in age from two to six years, with no significant departure from linearity.

The effect of age of dam becomes less and less pronounced as individuals approach yearling age, since they obtain more of their feed independently of their dams. Hence they tend partially to overcome earlier handicaps. Yearling lambs from two and three year-old ewes weighed 4.0 and 1.8 pounds less than lambs from four to seven years of age, a difference that is much less than the difference of 7.3 pounds at weaning in the case of two year-old ewes, but is about equal in the case of three year-old dams. However, when weaning weight was included in the model the effect of age of dam on yearling body weight was not significant. This reduction in the effect of age of dam on yearling weight was also observed by Terrill _et al_. (1947).

As for the yearling wool traits, age of dam was not a major source of variation. It reached significance in the case of grease and clean fleece weight and fiber diameter, but was not significant for staple length. Similar results have been shown by Rae (1950), Balch (1962), and Hall et al. (1964).

In this study sex of the lamb behaved contrary to the effects of age of dam and type of birth and rearing. That is, the sex effect was magnified with advancing age, and was significant at each stage. This was most noticeable for body weights. Sex effect accounted for 1.6, 3.5 and 27.9 percent of the total variability in birth, weaning and yearling body weights, respectively. Phillips and Dawson (1940) stated that the effects of sex on body weight at different stages were more pronounced as the lambs approached maturity. A part of the advantage that male lambs have over females at weaning is due to the difference in birth weights. This may be seen from the second model in which birth weight was included. Males exceeded females by 5.14 pounds at weaning in the first model, while the difference was reduced to 4.01 pounds when birth weight was included. This in turn will affect yearling body weight differences indirectly through their difference in weaning weight. Ram lambs exceeded ewe lambs by as much as 28.1 pounds as yearlings, this difference declining to 21.5 pounds when weaning weight was added in the model of analysis. De Baca et al. (1956) found that male lambs were heavier than ewe lambs at weaning. They also stated that a part of the advantage at weaning is a result of being heavier at birth.

Yearling ram lambs had 1.13 pounds more wool than ewe lambs, resulting in an excess of .75 pounds of clean fleece weight for males over females. This, of course, could very well be a result of heavier body weights, which in turn increases the body surface. Rams had 1.05 centimeters longer staple than ewes at shearing, with fiber diameter 1.42 microns larger. Terrill _et al_. (1947, 1948), in their study of yearling body and wool traits on Rambouillet sheep, found that rams weighed 44.2 pounds more than ewes, sheared 3.3 pounds more raw wool resulting in an advantage of 0.9 pounds of clean fleece estimated from small sample scouring. Staple length for rams was 1.2 centimeters longer than that for ewes. Comparable results were also obtained by the same authors for the Columbia and the Targhee breeds, with males always exceeding females. Rams might be more heavily selected than ewes, but the standard deviations were not much different in both sexes, being slightly higher in males than females in the majority of the traits studied. However, Balch (1962) found that rams sheared more wool than ewes, but had 0.4 centimeter shorter staple. This is contrary to what was found in this study and in the study of Terrill _et al_. These findings, added to those obtained in this work, could be due to different physiological functions in the two sexes, mainly attributed to hormonal differences that tend to become more pronounced as the animals approach maturity.

Of all the factors affecting birth weight, breeding group effect was the most important as it accounted for 18.5 percent of the total variance in birth weight. The Navajo breeding group was the smallest at birth, weighing 1.6 and 1.8 pounds less than lambs of the coarse-wool and fine-wool breeding groups, respectively, while the difference between these latter two groups was considerably smaller. These differences persisted until later weights. At weaning, the fine-wool breeding group was still heaviest, weighing 6.59 and 1.09 pounds more than the Navajo and the coarse-wool groups, respectively. However, a large part of this difference seems due to the advantage at birth, since the corresponding figures were 1.78 and .75 pounds in the second model for weaning weight. Yearling lambs of the Navajo breeding group were still the smallest, weighing 5.14 and 4.79 pounds less than the fine-wool and coarse-wool groups, respectively. This difference in weight was reduced to .75 and .72 pounds when weaning weight was included in the model for yearling body weight.

The Navajo breeding group, smallest in body weight, sheared lighter grease and clean fleeces. The fine-wool breeding group gave 2.01 and .74 pounds of grease fleece wool more than the Navajo and Coarse-wool breeding groups, respectively. However, due to a higher percentage of yolk in the wool, the fine-wool breeding group had .26 pounds less clean fleece weight than the coarse-wool group, but .66 pounds more than the Navajo. This was anticipated since finer wool usually shrinks more than coarser wool, as the latter has less yolk adhering to the wool fibers. The coarse-wool group also had the longest staple, followed by the Navajo and finally by the fine-wool group. As for the mean diameter of fibers, the fine-wool group had much smaller fiber diameter than either of the other two groups, with the coarse-wool and Navajo breeding groups not differing much in this respect. Wool suitable for carpet weaving requires a somewhat longer staple and coarser diameter than the fine wool fitted for use in the clothing industry.

The regression of weaning weight on age in days was .381 pounds. All the lambs in the flock were weighed at a set date, usually about the time the average age of lambs is close to 120 days, depending on management practice and other considerations prevailing in a given year. The age at weaning ranged between 95 and 145 days, with slight difference among years. In that sense, the regression of weight on age might be regarded as the growth rate of lambs in that period around weaning, depending on the extent to which growth rate is linear in that period. Warwick and Cartwright (1958) found that the regression of weaning weight on age in days was .3 pounds. They also reported that this regression was linear with very minor departure from linearity. Hazel and Terrill (1945a, 1946a) showed that the regression of weaning weight on age was of the order of .41 pounds for Rambouillet lambs and .45 pounds as a pooled estimate obtained from the Columbia, Corriedale, and Targhee breeds. Sidwell and Grandstaff (1949) studying Navajo sheep found that regression to be .37 pounds per day, which is in substantial agreement with the value found in this study. Other values reported in the literature ranged between .13 pounds per day obtained by Blackwell and Henderson (1955), to .55 pounds per day which MacNaughton (1956) found for the Rambouillet lambs.

When birth weight was included as a covariate (Model II) the regression of weaning weight on age at weaning increased to .45 pounds per day. A correlation coefficient of -.13 observed between birth weight and age at weaning could explain the increased regression. This means that lambs born later in the season had higher birth weights than earlier ones, which might be due to supplemental feeding given to dams shortly before lambing. Accordingly, ewes that lamb later in the season had a longer period of supplemental feeding before lambing.

The regression of yearling body weight on age in days was .169 pounds. This, as we mentioned previously, only pertains to the period of about 50 days that encompasses the 400 days age around which yearling weights were taken. Accordingly, this regression does not represent the average daily gain from birth to yearling age, but rather is the linear part of the rate of growth in the above mentioned period.

In the second model for yearling weight where weaning weight was included as a covariate, the regression of yearling weight on age changed its sign to a value of -.102 pounds. This indicates that for a constant weaning weight older animals gain less from weaning to yearling age than do younger animals. This also could mean that non-linearity does exist for the growth period between weaning and yearling age.

Hazel and Terrill (1946c) reported .031 pounds per day for the regression of yearling weight on age in Rambouillet ewes, while this regression was .186 and .296 pounds in Columbia and Targhee ewes, respectively (Terrill _et_ _al_., 1947). Price _et_ _al_. (1953) reported .12 pounds for that regression from data on Navajo ewes, which is in very good agreement with the value of .129 pounds found in this study for yearling ewes (Table 14). Hall _et_ _al_. (1964), working with yearling Navajo ewes, found that the regression on age was .101 pounds.

As for the yearling wool traits, the regressions on age at shearing were .026 and .012 pounds per day for grease and for fiber diameter were .017 centimeters and 0.33 microns, respectively.

Hazel and Terrill (1946) found that the regressions of grease and clean fleece weights on age in days for Rambouillet ewes were .026 and .011 pounds and that for staple length was .011 centimeter, which is in agreement with those found here. Price et al. (1953) observed a regression of .03 and .02 pounds per day for grease and clean fleece weights respectively, and .02 centimeters per day for staple length. Hall et al. (1964) using yearling ewes from the same source as the one at hand, obtained regressions on age at shearing of .022 and .014 pounds for grease and clean fleece weights, .017 centimeter for staple length and .016 microns for fiber diameter.

Birth weight had a highly significant effect on weaning weight which, in turn, affected the weight reached as a yearling. The regression of weaning weight on birth weight was 2.45 pounds and accounted for 5.14 percent of the total variability in weaning weight. Birth weight by itself is of small economic value, but could be a criterion for selecting animals to be kept until weaning, especially males. Moreover, Phillips and Dawson (1940) and others found that birth weight can indicate survival and growth. De Baca et al. (1956) found that the regression of weaning weight on birth weight varied from 2.50 to 5.96 pounds, and was the most influential of all variables affecting weaning weight. They also observed that the effect of birth weight was important on subsequent weights, since there was no overlap in the weight increase of lambs of a given birth weight and those of another. From the observed effect of birth weight on the other factors in the model, it seems that the advantages which single lambs, ram lambs, and lambs from older ewes have at weaning is partly due to their established advantage at birth.

Summing up, the environmental factors accounted for 49.5, 61.0, 79.9, 58.0, 56.4, 26.4, and 56.7 percent of the total variability in birth weight, weaning weight, yearling weight, grease fleece weight, clean fleece weight, staple length and fiber diameter. Adjustment for these factors is most important before estimating phenotypic and genetic parameters from the data. Staple length was least affected by these factors, while yearling body weight was the most strongly affected by them. It is evident that the weight of the individual becomes more and more affected by its surrounding and inherent environment with the progress of age.

Table 14 gives the least squares estimates obtained from the analysis of the records of the ewes only, for comparison with those from the combined data.

The phenotypic correlations computed in this study and reported in Table 20 show that animals with heaviest weights at birth also tended to have heavier subsequent weights. Heavier animals also tended to produce more wool with thicker, but somewhat shorter fibers. Correlations between the wool traits were generally positive and of moderate size, except for a small negative correlation between fiber diameter and staple length. This latter result may be due to the restricted food supply generally prevailing under the Southwest range conditions.

The high positive correlation between grease and clean fleece weights was anticipated since it is a past-total correlation. The relationship which exists between clean fleece weight and grease fleece weight, staple length and fiber diameter has been used by many workers to predict clean fleece yield from these other variables. Yield determination is one of the most tedious and expensive operations required in evaluating the wool production of individual animals. Terrill _et al_. (1945) showed that clean fleece weight could be estimated from grease fleece weight and staple length almost as accurately as from scouring a small side sample from the fleece. They obtained a multiple correlation coefficient of .81 from analyzing 1037 Rambouillet fleeces, and slightly higher values in the other breeds studied. Price _et al_. (1964) also found results which confirmed these obtained by Terrill _et al_. for predicting clean yield from other wool traits. They commented that this method gave good and consistent predictions, but that constants should be evaluated for each flock where the method is used. Sidwell et al. (1956) found that including grease fleece weight and staple length only in a prediction equation to determine clean fleece weight was accurate enough for practical purposes, the multiple correlation being .89.

The values obtained for the phenotypic relationship between clean fleece weight and the other wool traits agree with those reported in the literature (Table 2). These correlations also indicate the possibility of predicting clean yield from the other wool components.

The phenotypic correlations are of moderate positive size, but this does not indicate that selecting for one of these traits will automatically result in progress or hindrance in the other correlated ones. This is because the correlations that should apply in this situation are the genetic correlations rather than the phenotypic ones. The environmental effects upon two traits could be so strong and positively correlated that a negative genetic correlation is overshadowed and a positive phenotypic correlation is the end result.

B. Genetic Statistics

The estimates of heritability found in this study agree with those reported in the literature rather well, considering the extreme environment under which the flock had been raised. Weather and grouping conditions in New Mexico were considerably different from those experienced under farm and Northwestern range conditions. Management practice is about the same as that for sheep raised under range conditions in the United States Northwestern states, but with much difference in temperature and rainfall. Since the genetic statistics obtained in this study pertain to sheep of unusual genetic origin which were kept under severe environmental conditions, the observed values are not supposed to represent estimates of species or even breed constants. On the other hand, they should provide useful estimates of the magnitude of these statistics in this flock and in similar flocks. The relative importance of sources of variation may differ, depending on the control of variability due to the adjustable factors, and the gene frequencies in the studied population.

As mentioned in IV-B, heritability was estimated using two methods, i.e. (1) correlation between paternal half-sibs, and (2) intra-sire regression of offspring on dam. Since the year in which the ewe was born could be a source of bias in the second method, another estimate of heritability was obtained in which this source of bias was eliminated by calculating the regression of offspring on dam from the sums of squares and cross-products from the differences within years of birth of the dams. It is noticeable that all of the heritability values obtained from the regression method are higher than their counterparts calculated from the paternal half-sib correlation method, with the exception of that for clean fleece weight. These higher estimates by the regression method are so noticeable that the possible cause should be enumerated.

More intense selection of rams than ewes could reduce the correlation between paternal half-sibs by decreasing the variability in the sires more than that in the dams. Selection has to be exceedingly powerful to result in such reduction. Rowe (1964) in a study of simulated data showed that very intense selection is needed before an estimate of heritability of the order of .25 will be reduced by as much as .05. However, heritabilities of higher magnitude would be more strongly affected by selection intensity than those with lower values. For example, the same degree of selection as mentioned above reduced a heritability value of .50 by as much as .15.

Epistatic effects derived from a large additive X additive component of variance would result in an upward bias of the heritability obtained from regression of offspring on dam compared with that from the half-sib correlation method. The regression method contains one-fourth more of the additive X additive variance than does the half-sib method.

Maternal effects could also contribute to the observed regression of offspring on dam, while they would not to the half-sib correlation. This factor will tend to bias the regression estimate upwards more frequently than downwards. For example a tendency for heavier dams at yearling age to produce heavier offspring would increase the resemblance between dam and offspring. A part of this may be eliminated by type of birth or age of dams correction factors, but there seems to be no reason for thinking all of the maternal influence would be eliminated in this manner. This maternal effect could be either of environmental or genetic origin of which the extreme of the latter is the cytoplasmic inheritance. Obviously, maternal effects do not influence the resemblance between paternal half-sibs unless assortive mating is being practiced or dams are related. Many situations had been reported in the literature which showed the importance of such maternal influences.

The difference between the two estimates of heritability found in this study are probably due to a combination of some of the factors discussed and possibly others. When the above factors are important enough to have measurable influence, the heritabilities calculated from the paternal half-sibs data are likely to be smaller than those based on offspring-dam regression method.

Many workers who have obtained estimates of heritability from both methods have found results that agree in part with those found here. Ali (1952) found that the heritability of birth weight was .19 from the correlation method, while the estimate from regression was .54. Corresponding figures for the heritabilities of weaning weight were .14 and .38 and for grease fleece weight .27 and .51. Yao et al. (1953) reported an estimate of .18 for the heritability of birth weight from the half-sib correlation method, and .35 from the regression method. Hazel and Terrill (1945b) reported values of .27 and .34 for weaning weight from the correlation and regression methods, respectively. Morley (1951, 1955) obtained the corresponding estimates of .21 and .36 for heritability of shearling body weight, .26 and .47 for clean fleece weight, .09 and .36 for yearling weight, and .52 and .56 for staple length. Bradford and Van Vleck (1964) found similar situation with milk production. The estimates of heritability of milk production were .25 and .44 calculated from the paternal half-sib correlation and the regression of daughters on dam methods, respectively.

However, other studies show that the estimates obtained from the half-sib correlation method were higher than those from the regression method. Hazel and Terrill (1945b) reported two heritability estimates of .41 and .39 for staple length calculated from the correlation and regression methods, respectively. Morley (1951) found that the heritabilities of grease, clean fleece weights, and staple length were .39 and .67, .62 and 1.02, and .22 and .24 calculated from the regression and the correlation methods, respectively. Shelton and Campbell (1962) obtained estimates of .19 and .30 for the heritability of weaning weight from the regression and correlation methods, respectively.

When genotype-environment interactions are important the half-sib correlations, as estimated from variance components, might give higher estimates than the regression method, since half-sibs are contemporaries and share the same yearly climatic conditions and environments. Dam and offspring, on the other hand, express their traits in different years and genetic-environmental interactions are unlikely to appear in their covariance.

The differences between the heritability estimates, obtained from both the correlation and the regression methods, were larger with body weights than with the wool traits. This may be due to selection being practiced largely for weight, especially at weaning. This seems unlikely since heritability would have to be unreasonably high for this to happen. The effect of maternal environmental correlation would also be likely to appear more strongly for body weights than for fleece traits.

Tables 21 and 22 show the analysis of variance and heritabilities obtained from analyzing the data on ewes only by the paternal half-sibs correlations method, for the five yearling and wool traits. All the estimates obtained were

Table 21. Analysis of variance of adjusted records obtained from ewe data

Source of variation	Degrees of freedom	Yearling weight		Grease fleece weight	
		Mean square	Variance component	Mean square	Variance component
Between breeding groups-years	32	5599.7	156.58	30.05	.80
Between sires/ breeding groups-year	152	79.1	4.05	1.68	.16
Within sires	1004	54.2	54.15	0.67	.67
Total	1188				

Expected mean squares are

Between breeding groups-years $\sigma_e^2 + K_2\ \sigma_s^2 + K_3 K_{BY}^2$

Between sires/breeding groups-years $\sigma_e^2 + K_1\ \sigma_s^2$

Within sires σ_e^2

and $K_1 = 6.17$

Table 21. (Continued)

Source of variation	Clean fleece weight		Staple length		Fiber diameter	
	Mean square	Variance component	Mean	Variance component	Mean	Variance component
Between breeding groups-years	7.60	.198	49.07	1.31	329.57	9.09
Between sires/ breeding groups-year	0.54	.050	2.81	0.13	8.11	.60
Within sires	0.23	.233	1.98	1.98	4.43	4.43

Expected mean squares are

Between breeding groups-years	$\sigma_e^2 + K_2\ \sigma_s^2 + K_3 K_{BY}^2$
Between sires-breeding groups-years	$\sigma_e^2 + K_1\ \sigma_s^2$
Within sires	σ_e^2

and $K_1 = 6.17$

Table 22. Heritabilities estimates obtained from analysis of variance of ewe data

Trait	Heritability	Standard error
Yearling weight	.280	±.100
Grease fleece weight	.780	±.132
Clean fleece weight	.704	±.128
Staple length	.252	±.100
Fiber diameter	.476	±.116

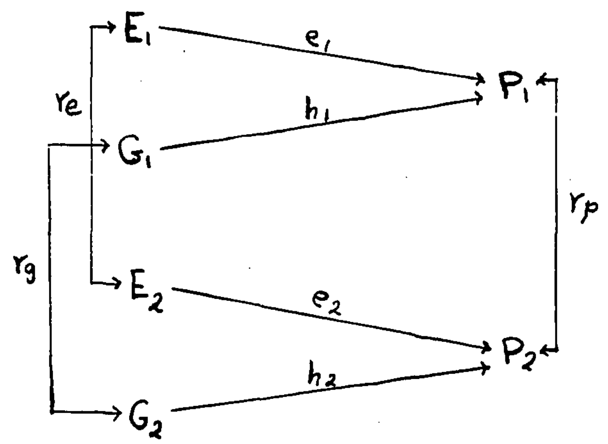
higher than those obtained from the analysis of the combined data which included both rams and ewes. If the two sexes are considered as different environments, the lower estimates from the combined data can be regarded as the result of a genotype-environmental interaction. This amounts to saying that some of the genes contributing to the observed variations in the traits studied have different expressions in the two sexes, even where the average sex differences have been removed.

Sex-linked factors would contribute to the resemblance between paternal half sisters but not to paternal half brothers, but their contribution to the dam-offspring covariance would be equal in both sexes of offspring.

The values obtained for the heritabilities of the different traits indicate that considerable improvement can be achieved by mass selection for any of the traits studied. Wool traits in particular should respond noticeably to mass selection.

However, in real situations selection would seldom be directed towards one trait only, but rather to a number of traits that are of economic importance. If we select for more than one trait the net progress in both will depend to a certain extent on the relationship between these two traits. The part of the relationship between two traits that may affect the outcome of selection is the genetic part or the genetic correlation between the two traits. Lush (1948) has suggested that past selection for two or more traits is likely to have caused the present genetic correlation to become negative rather than positive, if the direction of selection was towards increasing both traits. As mentioned before in II-D the most important cause of genetic correlation between traits is that due to the pleiotropic effects of genes. An inherent part of this hypothesis is that selection has been so effective in the past that it has driven genes with favorable effects upon both traits to frequencies near unity. Genes that will affect one trait favorably and another unfavorably will tend to stay at intermediate frequencies and thus be responsible for the most of the present genetic variability.

It is possible for positive phenotypic correlation to exist between two traits, while they have a negative genetic correlation. The relationship between the phenotypic, genetic, and environmental correlations, between two traits, could be illustrated by the following path coefficient diagram and pertinent formula assuming no genotype-environment interaction



then

$$r_p = r_g\, h_1\, h_2 + r_e\, e_1\, e_2$$

where r_p, r_g, and r_e are the phenotypic, genetic, and environmental correlations between traits 1 and 2 and their heritabilities are h_1^2 and h_2^2, respectively, and $e_1 = 1\text{-}h_1$, $e_2 = 1\text{-}h_2$.

If r_e is high and positive, and heritabilities are low then r_p can be positive and r_g negative.

Another situation that might exist is for the phenotypic correlation to be positive but less than the genetic correlation. This could happen if the environmental correlation between both traits has a small positive value.

The environmental correlations are due to non-identifiable factors since those that were known have been adjusted. As such the remaining environmental factors are likely to be more temporary in nature, and animals are exposed to many transient effects which may be either positive or negative. But genetic effects are more permanent in nature since animals have the same sets of genes throughout life and these effects change only when physiological processes change in the course of development. This reasoning leads to the hypothesis that genetic correlations could be larger than environmental correlations, but gives no real hint as to what their direction may be.

The situation found here for the genetic and phenotypic correlations between weaning weight and yearling body weight illustrates the situation described above. The estimate of the genetic correlation between them was greater than unity. Sampling errors could be a cause for it being so large, but certainly the genetic correlation between these two traits is very high and might be really near unity. This might be because the genes that control growth between birth and weaning are the same genes that affect post-weaning growth, which is what is meant by pleiotropy. On the other hand, the pre-weaning environment of the lamb is concentrated around his mother and her ability to produce milk is his primary source of nutrition. However, after weaning the lamb is exposed to a new environment and depends upon his own resources for nourishment. These two sets of environment could be widely different and seem to be nearly independent of one another.

Searle (1961) and Van Vleck (1960) found a similar situation for the correlation between milk yield in the first month of a cow's lactation and the total lactation yield. Givens et al. (1960) found the phenotypic correlation between 120 day weight and daily gain to be .86 while the genetic correlation was 1.08. They stated that although too large, the genetic correlation indicates the two traits are measuring the same effect. Hall et al. (1964) reported a value of .93 for the genetic correlation between grease fleece weight and clean fleece weight while the phenotypic correlation was between .66 and .75. MacNaughton (1956) found a genetic correlation of .51 between birth and yearling weights while the phenotypic correlation was .37.

The estimates of the genetic correlations obtained in this study using the two formulas mentioned, indicate that there is a predominant negative correlation between the body weight at different stages and the wool traits. If selection is based on weaning weight at weaning time we are liable to cull some individuals that would have been kept had we known their wool yields. The existence of a negative correlation between those traits will prevent the occurrence of many individuals that are superior in both traits. Since lambs are not sheared at weaning their potential for wool production is not known, and capability for wool production may not receive much attention at weaning. A way around this is to use staple length and fiber diameter which show earlier in life and are correlated to a certain extent with grease and clean fleece weights. Of course it would be better if all lambs are kept until their yearling wool production is obtained, but this will put a great burden on the available grazing area and increase labor and management requirements, and could render such practice not profitable at the end, compared with the expected genetic gain.

Body weights at different stages were positively correlated to a moderate extent, so are yearling wool traits, except, of course the high positive correlation between clean and grease fleece weight. Table 3 shows the genetic correlations that were reported in the literature for comparison with those found in this study. Hall <u>et al</u>.(1964), working with data on yearling ewes from the same source as at hand observed the prevailing negative genetic correlations between body weight and wool traits. Both findings indicate that selection for increased wool weight will result in a decrease in body weights, and vice versa. A reason for that may be that the limited amount of available protein will be either diverted for body growth or to wool growth according to how the genes that govern body and wool compete for the available protein. Slen and Whiting (1952) found that grease fleece weight, clean fleece weight, fiber length and fiber thickness increased with the increase in the level of protein from 7 to 10 to 13 percent of the diet. It seems reasonable that where the level of protein in the diet was increased, the negative correlations between body and wool traits would be smaller and might even assume positive values if the requirements for the growth of wool and body were all satisfied and competition between the genes governing these traits were eventually eliminated. Verification of this hypothesis would require studying the genetic correlations at different levels of protein diet.

The existing breed differences in average wool and lamb production also reflect the genetic correlations found in this study. Merinos are usually slower in growth than the related heavier Rambouillet breed, but the former excels in staple length and clean fleece production. Similarly the fast-growing Down breeds usually produce shorter and finer wool than the long wool breeds, which are slower in their rate of growth.

VII. SUMMARY AND CONCLUSION

This investigation was mainly aimed at estimating the phenotypic and genetic parameters of sheep that are raised under arid conditions. Of interest also were he effects of known environmental factors on these sheep as compared with the effects of similar factors on sheep kept under more favorable conditions.

Data were studied on 3264 lambs born in consecutive years from 1950 through 1961 from an experiment at the Southwestern Range and Sheep Breeding laboratory at Fort Wingate, New Mexico. All the sheep used were derived from the Navajo breed, originally maintained by the Navajo Indians and the surrounding tribes. Three distinct breeding groups were formed from the original Navajo breed. These are the Navajo, Fine wool and Coarse wool breeding groups, the last two being developed by crossing ewes of Navajo origin to sires of different breeds. Selection was directed towards improving wool and mutton qualities in the three breeding groups, with special emphasis on carpet wool qualities in the coarse-wool breeding group, and on commercial wool qualities in the Finewool group.

The traits studied were birth weight, weaning weight, yearling body weight, grease fleece weight, clean fleece weight, staple length and fiber diameter. Larger numbers of animals were available on the first two traits than on the yearling wool and body characters.

The fixed effects studied were year of birth, breeding group, type of birth and rearing, age of dam, sex, and age of the individual in days (Model I). In addition, the effect of the individual's birth weight on his weaning weight, and the effect of the individual's weaning weight on his yearling body and wool traits were included as second models.

All the fixed factors proved to have significant effects on all of the seven traits studied with the exception of the age of dam effect on staple length and the type of birth effect on fiber diameter. Environmental factors were found to differ in their importance on the different traits, with some being important at early ages and then decreasing as the lambs become older, while others were important for traits that show later in life. Factors that are related to maternal environment, such as type of birth and age of dam, were most important on birth and weaning weights. Yearly effects, reflecting feed conditions, and sex-related differences influenced yearling traits more than weanling traits. Breeding group differences were important at all stages of life and for all traits.

Heritabilities were obtained from paternal half-sib correlations and from the regression of offspring on dam. Both analyses were performed within sires, years and breeding group. The estimates obtained were:

	Paternal half-sibs	Regression of offspring on dam
Birth weight	.22	.37
Weaning weight	.21	.29
Yearling weight	.19	.53
Grease fleece weight	.43	.49
Clean fleece weight	.40	.31
Staple length	.20	.33
Fiber diameter	.20	.41

Possible reasons for the differences between the estimates obtained by the correlation and regression methods have been discussed. The data on ewes alone were used to obtain heritability, and the possible reasons for differences between values obtained from both sexes have also been mentioned.

Genetic and phenotypic correlations between all studied traits were given in Tables 18 and 20. Moderate positive genetic correlations were obtained between body weights at different ages and also between wool traits, except for a high positive correlation between weaning and yearling weights and a high one between clean and grease fleece weights. Negative genetic correlations were observed between body weights and the wool traits. Selection for increased body weights could lead to a decrease in clean fleece weight, staple length and fiber diameter.

The results indicate that an appreciable portion of the total variability is due to the additive effects of genes. Consequently mass selection should permit measurable progress.

Genetic correlations should be considered when selecting animals because of the antagonistic body weight-wool relationships.

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